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An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys

The late W. F. Whittard, F.R.S.
(Compiled by W. T. Dean)

Geology series Vol 33 No 1 20 December 1979

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An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys

The late **W. F. Whittard,** F.R.S.
(Compiled by W. T. Dean, Department of Geology, University College, Cardiff, CF1 1XL)

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Synopsis

On the basis of the late Professor W. F. Whittard's field maps and notes, a geological map, scale 1 : 32 000, is presented for the Ordovician rocks of the Shelve Inlier. These strata, excluding the Shineton (or Habberley) Shales of Tremadoc age, range from lower Arenig Series to lower Caradoc Series. The history of the lithostratigraphic classification is reviewed, and a scheme of three formations and fifteen members proposed on the basis of already-named subdivisions. Descriptions are accompanied by enlarged sketch maps showing outcrops and relevant fossil localities. A slightly revised correlation table is included, together with a table showing characteristic trilobites. Geological structure and igneous rocks (all known outcrops of which are shown on the map) are briefly discussed.

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The late Professor W. F. Whittard, F.R.S.
1902–1966

Introduction and Acknowledgements

The task of mapping and describing the Ordovician rocks and faunas of the Shelve Inlier was begun by Professor W. F. Whittard (frontispiece) in 1930 as a sequel to work on the Lower Silurian rocks of the same area. From then until his untimely death early in 1966 the Shelve Inlier occupied the greater part of his research time and was frequently visited by him with mapping classes from the University of Bristol. Although the Ordovician rocks of the Inlier have yielded large numbers of fossils – and Whittard's beautiful monograph (1955) on the trilobites, published by the Palaeontographical Society, is a classic of its kind – they are rarely obviously fossiliferous to the casual visitor, who may find collecting both difficult and unrewarding. Much of Whittard's time on the Inlier, particularly during the early years, was spent collecting fossils in an attempt to define the faunal content of the numerous lithostratigraphic subdivisions established earlier, principally by Lapworth & Watts (1894), and it was not until the appointment of Mr T. R. Fry as Whittard's research assistant that the time-consuming task of fossil-collecting was eased. Fry displayed a remarkable aptitude for obtaining faunas from even the most unpromising strata and his contribution received appropriate recognition when the University of Bristol awarded him the honorary degree of M.Sc. in 1970. In later years he was ably assisted by Mr M. White and both had trilobite species named after them by Whittard.

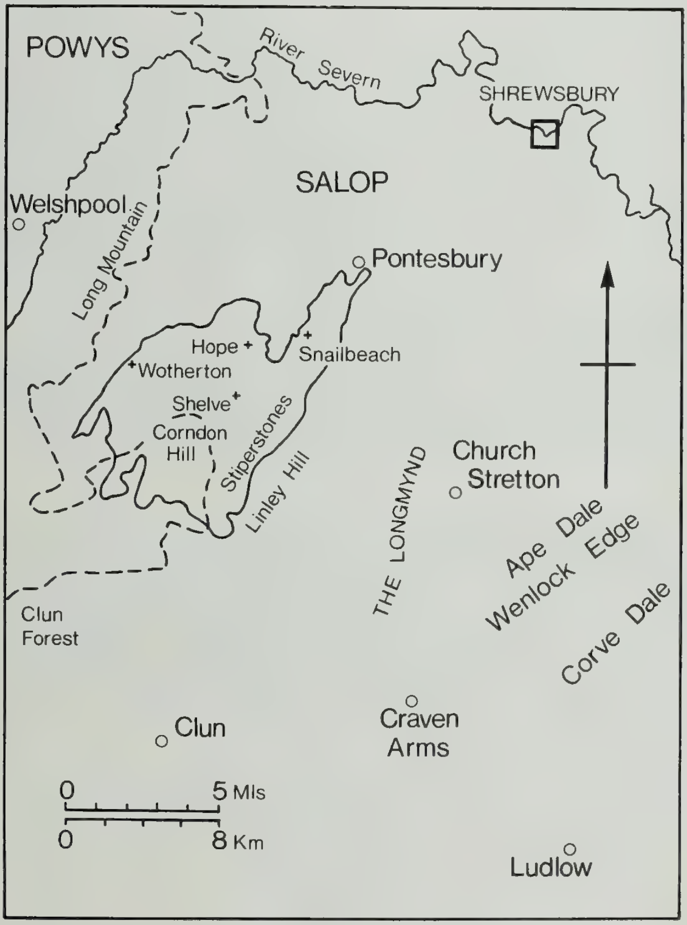
POWYS
River Severn
SHREWSBURY
SALOP
Welshpool
Long Mountain
Pontesbury
Hope
Wotherton
Snailbeach
Shelve
Corndon Hill
Stiperstones
Linley Hill
THE LONGMYND
Church Stretton
Ape Dale
Wenlock Edge
Corve Dale
Clun Forest
Clun
Craven Arms
Ludlow
0
5 Mls
0
8 Km

Fig. 1 Sketch map of part of the Welsh Borderland showing the position of the Shelve Inlier in relation to various towns and topographic features.

Whittard's mapping of the Ordovician rocks in the Shelve Inlier formed a natural sequel to his well-known mapping and highly original interpretation of the Lower Silurian strata of the region. He noted that the lack of cleavage affecting the Ordovician rocks, together with their relatively abundant fossils, not always readily apparent during brief visits, showed the palaeontological promise to be much greater than previously published accounts might have led one to believe. Furthermore, the rich trinucleid trilobite faunas suggested to him that the Shelve succession might become the standard for the Lower and Middle Ordovician of the Anglo-Welsh area, a sentiment expressed earlier with equal confidence by Lapworth (1887 : 663), while the not infrequent intermixing of shelly fossils and graptolites held out hope for the solution of numerous correlation problems.

At the time of Professor Whittard's death the Shelve trilobite monograph was almost complete, lacking only a final chapter (since completed, Dean 1967) on the affinities of the trilobites; more recently the brachiopods have been described by Williams (1974) and the graptolites are being studied by Dr Isles Strachan. A large proportion of the mapping had been completed at a scale of 6 in to 1 mile (1 : 10 560) and the results entered upon Quarter-Sheets mounted on cloth. Unfortunately several gaps remained on this version of the geological map, particularly in complex areas where more than one interpretation is possible, and it has been my object to try to fill these gaps utilizing Whittard's field slips, some of which are at a scale of 25 in to 1 mile (1 : 2534·4). No systematic account of the Shelve Inlier's geology had been prepared but notes on a large number of Ordovician localities are contained in Whittard's meticulous field notebooks and I have drawn extensively upon these in preparing the Ordovician stratigraphic account. Consequently most of the geological observations and conclusions in the present paper are attributable to Professor Whittard but in addition numerous publications are quoted in an attempt to formulate a coherent account of the Inlier, and any shortcomings in drawing the two sets of data together are my own responsibility. It had clearly been Whittard's intention to make his description of the Shelve Inlier as comprehensive as possible, including chapters on geological structure, igneous activity and mineralization, but as no such accounts had been prepared I have preferred to keep these sections to a minimum.

All the measurements are given in British Imperial units, as originally made by Whittard; metric equivalents are appended in every case.

The small geological maps reproduced as figures in the text are at a scale of 4 in to 1 mile (1: 15 840); grid squares are indicated. The photographs are from colour transparencies taken by Whittard; all the places named may be found with reference to points shown in the large Map.

The numbered localities refer to Whittard's manuscript notes.

Geographical location and Previous researches

The Ordovician rocks of the Shelve Inlier form an irregular area (Fig. 1) of some 43 mile^2 (111 km^2) centred approximately on Shelve, an otherwise obscure hamlet situated *c.* 21 km (13 miles) SW of Shrewsbury. Most of the inlier is located within the bounds of west Salop (formerly Shropshire), but the area in the south-west, comprising Corndon Hill, Todleth Hill and Church Stoke (Fig. 2), forms part of the adjacent Welsh county of Powys. Topographically the area is one of rapidly-changing relief, drained by the Rivers Camlad and West Onny together with numerous streams which exhibit a suggestion of a radial pattern. The highest points are found at Corndon Hill (1683 ft, =513 m) and the Stiperstones (up to 1762 ft, =537 m), the latter bounding the sombre, marshy area of The Bog and forming an impressive rampart which achieved some literary recognition in Mary Webb's novel 'Gone to Earth'. The region is sparsely inhabited and villages and hamlets are relatively few, the most notable being Chirbury, Hope, Old Church Stoke, Priestweston, Rorrington and Wotherton. In Roman times the area around Shelve and Ritton Castle was the site of important lead mines and lead mining continued until early in the 20th century; it has since been discontinued but exploitation of barytes in the old tip heaps continues sporadically at the present day. Notable view-points are Bromlow Callow (Map) and the top of Priest Weston Bank from which can be seen a panorama that includes Plynlimmon,

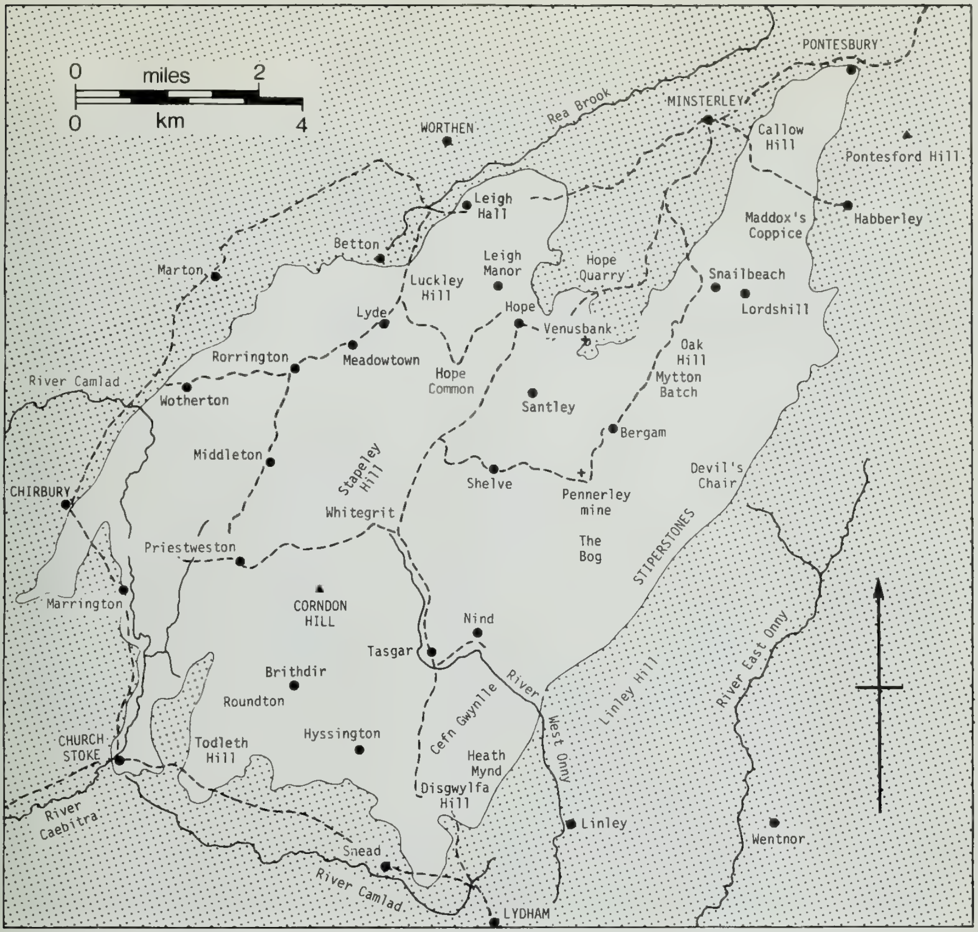
0
miles
2
0
km
4
PONTESBURY
MINSTERLEY
Rea Brook
WORTHEN
Callow Hill
Pontesford Hill
Leigh Hall
Maddox's Coppice
Habberley
Betton
Leigh Manor
Hope Quarry
Marton
Luckley Hill
Snailbeach
Lordshill
Lyde
Hope
Venusbank
Rorrington
Meadowtown
Oak Hill
River Camlad
Hope Common
Mytton Batch
Wotherton
Santley
Bergam
Middleton
Stapeley Hill
Shelve
Devil's Chair
CHIRBURY
Whitegrit
Pennerley mine
STIPERSTONES
The Bog
Priestweston
CORNDON HILL
Marrington
Nind
River East Onny
Tasgar
Brithdir
River
Linley Hill
Roundton
Cefn Gwynlle
West Onny
CHURCH STOKE
Todleth Hill
Hyssington
Heath Mynd
Disgwylfa Hill
River Caebitra
Linley
Wentnor
Snead
River Camlad
LYDHAM

Fig. 2 Outline map of the Shelve Inlier to show the location of principal place-names mentioned in the text.

Cader Idris, the twin Peaks of the Arenigs, Berwyn and, to the north, the Cheshire Plain with its girdle of Bunter Sandstone (Trias) hills such as Grinshill, Hawkstone and Nesscliff. From the Stiperstones all these are visible and, in addition, the Uriconian hills of the Church Stretton area showing over the top of the Longmynd, the isolated Uriconian mass of the Wrekin to the north, and the successive Silurian escarpments running away from view to the south.

Work on the Ordovician rocks of the Inlier dates from the time of Murchison and a brief chronicle of subsequent researches was given by Whittard (1931 : 332; 1952) and, with particular reference to the trilobites, in the first part of his monograph (1955 : 1). As he noted, the first geological maps of the region were provided at a scale of 1 in to 1 mile (1 : 63 360), although a detailed 6 in to 1 mile (1 : 10 560) map by Lapworth & Watts remained unpublished except for a reduced and 'slightly modified' version which appeared in the Geological Survey's regional guide to the Welsh Borderland (Pocock & Whitehead 1948 : pl. 11; Earp & Hains 1971 : pl. 4). The frequent alternation of resistant bands of the Whittery, Hagley and Stapeley Volcanic Members, and quartzites of the Stiperstones Member, with soft shaly bands that are also often present within the volcanics themselves, gives rise to a ribbed topography which quickly shows any displacement caused by faulting. The innumerable breaks in the run of these hard rocks, associated

LAPWORTH, 1887	
Marrington Group	Whittery Ashes & overlying shales
	Hagley Volcanic Ashes & Shales
Aldress Group	Aldress Graptolitic Shale
	Spy Wood Calcareous Grit
Rorrington Group	
Middleton Group	
Weston Group	
Stapeley Volcanic Group	
Ladywell Group	
Stiper Group	
Cambrian	

LAPWORTH & WATTS, 1894		
Chirbury Series	Marrington Group	Whittery Shales
		Whittery Ash
		Hagley Shales
		Hagley Ash
	Spy Wood Gp	Aldress Graptolitic Shale
		Spy Wood Grit
Meadowtown Series	Rorrington Flags	
	Middleton Group	
	Weston Group	
Shelve Series	Stapeley Ashes	
	Hope Shale Group	
	Mytton Group	
	Stiper Stones Quartzite	
Shineton Shales		

LAPWORTH & WATTS, 1910		
Chirbury Series	Marrington Group	Whittery Shale
		Whittery Ash
		Hagley Shale
		Hagley Ash
	Spy Wood Gp	Aldress Shale
		Spy Wood Grit
Middleton Series	Rorrington Shales	
	Meadowtown Calcareous Beds or Stage	
	Betton or D. murchisoni Shales	
	Weston Flags & Shales	
Shelve Series	Stapeley Ashes	
	Hope Shales	
	Mytton Flags	
	Stiper Quartzite	
Shineton Shales (conformable)		

LAPWORTH, 1916		
Chirbury Series	Marrn Group	Marrington or Whittery Shales
	Hagley Group	Whittery Ash
		Hagley Shales
		Hagley Ash
	Aldress Group	Dictyonema Band, L. sericea Bands, Climaco. & Dicrano. Beds, Beyrichia Grits
Middleton Series	Rorrington Gp	Leptograptus Beds
		Nemagraptus Beds
	Meadowtown Gp	Ogygia Shales (Mount Beds)
		Meadowtown Lst, Flags Ogygia Flags
	Betton Gp	Didymograptus murchisoni Beds
	Weston Gp	L. & U. Weston Grits Weston Shales
Shelve Series	Stapeley Group	Upper Stapeley Shales
		L, M & U Ashes L & M Shales
	Hope Gp.	L, M & U Hope Shales & Chinastone Ash
	Mytton Group	Tankerville Flags & Shales
		Ladywell, Snailbeach Sh., Lord's Hill Beds
		Stiper Stones (Quartzite)
		Habberley Shales (conformable)

WATTS, 1925		
Chirbury Series	Marrn Stage	Whittery Shales
	Hagley Stage	Whittery Ash
		Hagley Shales
		Hagley Ash
	Aldress Stage	Shales with Dictyonema, etc
		Beyrichia Grit
Middleton Series	Rorr'n Stage	Leptograptus Beds Nemagraptus Beds
	M'town Stage	Ogygia Shales Lsts & Flags Ogygia & Asaphus Flags
	Betton St	D. murchisoni Beds
	Weston St	Grits & Shale
Shelve Series	Stapeley Stage	Alternating sequence of 3 lavas and 3 shales
	Hope Stage	L, M & U Shales & Chinastones
	Mytton Stage	Tankerville Flags
		Shelve Church Beds, etc.
		Stiperstones Quartzite
Habberley Shales (conformable)		

Fig. 3 Series of tables showing the progressive development in Ordovician

with high dips approaching the vertical, soon demonstrated that the inlier is traversed by tear-faults which, in the present paper, are shown to possess a remarkably uniform pattern. Whittard's notes emphasize that most of these tear-faults, which constitute such a dominant structural feature of the inlier and were reviewed by him (Whittard 1952 : 186, *et seqq.*), had not been recognized by Lapworth & Watts. A point reiterated in the notes is that such structures could only be mapped satisfactorily on the basis of a detailed knowledge of the stratigraphical palaeontology, so that it became possible to differentiate between sets of outcrops which, although lithologically distinct (and therefore true lithostratigraphic subdivisions) when clear sections were available, nevertheless posed considerable problems of identification when seen only in the form of small, weathered outcrops of shattered rock.

Geologically the inlier is bounded on the east by the Pre-Cambrian (Western Uriconian and Longmyndian) rocks of the Longmynd and adjacent areas, which are separated from the Shineton Shales of the Habberley Valley by a major structural line, the Linley–Pontesford Fault. The latter was not shown on Whittard's manuscript map but for the sake of giving a more complete geological picture is included here together with certain details of the Linley and Pontesford districts taken from papers by James (1956) and by Dean & Dineley (1961). The southern boundary is formed by the overstep at the base of the unconformable Lower Silurian

WHITTARD, 1931		WHITTARD, 1940	WHITTARD, 1952	WHITTARD, 1955		WHITTARD, 1966	PRESENT PAPER	
Marring-ton St.	Whittery Shales	Whittery Shales	Whittery Shales		Whittery Shales with Volcanic Gp.	Whittery Shales	CHIRBURY FORMATION	Whittery Shale Member
Hagley Stage	Whittery Volcanic Group	Whittery Volcanic Gp.	Whittery Volcanic Gp.			Whittery Volcanic Gp.		Whittery Volcanic Member
	Hagley Shales	Hagley Shales	Hagley Shales		Hagley Shales and Volcanic Gp.	Hagley Shales		Hagley Shale Member
	Hagley Volcanic Group	Hagley Volcanic Gp	Hagley Volcanic Gp			Hagley Volcanic Gp		Hagley Volcanic Member
Aldress Stage	Aldress Shales	Aldress Shales	Aldress Shales		Aldress Shales	Aldress Shales		Aldress Member
	Spy Wood Grit	Spy Wood Grit	Spy Wood Grit		Spy Wood Grit	Spy Wood Grit		Spy Wood Member
Rorr-ington Stage	Rorrington Beds	Rorrington Beds	Rorrington Beds		Rorrington Beds	Rorrington Beds	MIDDLETON FORMATION	Rorrington Member
Meadow-town Stage	Meadowtown Beds	Meadowtown Beds	Meadowtown Beds		Meadowtown Beds	Meadowtown Beds		Meadowtown Member
Betton Stage	Betton Beds	Betton Beds	Betton Beds		Betton Beds	Betton Beds		Betton Member
Weston Stage	Weston Grits & Flags	Weston Beds	Weston Beds		Weston Beds	Weston Beds		Weston Member
Stapeley Stage	Stapeley Shales	Stapeley Shales	Stapeley Shales		Stapeley Shales	Stapeley Shales	SHELVE FORMATION	Stapeley Shale Member
	Stapeley Volcanic Group	Stapeley Volcanic Gp	Stapeley Volcanic Gp		Stapeley Volcanic Gp	Stapeley Volcanic Gp		Stapeley Volcanic Member
Hope Stage	Hope Shales & Chinastone Ash	Hope Shales	Hope Shales		Hope Shales with Chinastone Ash	Hope Shales		Hope Member
Mytton Stage	Mytton Flags	Mytton Flags	Mytton Flags	Mytton Flags	Tankerville Flags	Tankerville Flags		Mytton Member
					Shelve Church & Lord's Hill Beds	Mytton Flags		
	Stiperstones Quartzite	Stiperstones Quartzite	Stiperstones Quartzite		Stiperstones Quartzite	Stiperstones Quartzite		Stiperstones Member
Habberley Shales		Habberley Shales	Tremadocian		Habberley Shales	Habberley Shales	Shineton Shales	

ithostratigraphic terminology for the Shelve Inlier from 1887 to the present.

rocks. Similar Silurian strata form the northern boundary but extend farther across the Ordovician outcrop and are in turn overstepped by the unconformable base of the Coal Measures of the Hanwood Coalfield. The relationships of these overlying Silurian and Carboniferous rocks are much obscured by glacial deposits and by alluvium of Habberley Brook, River West Onny, River Camlad, and Aylesford and Rea Brooks. The western boundary of the inlier is still more obscured and it is possible that additional, and younger, Ordovician strata may underlie the cover of superficial deposits. Whittard's unpublished notes on this area include the following paragraphs:

> Excluding the exposures of Hagley Shales in the village of Church Stoke, there are no localities on the west of the Church Stoke – Chirbury road and south of the road from Alport to Cross House, Rhiston and Upper Grwarhlow where any solid rock can be examined. Much of this area is about 500 ft (152 m) O.D. and topographically it is composed of an eastward-trending ridge which is aligned at right-angles to any known strike in the Ordovician rocks or expected strike in the Silurian rocks, and since there is much boulder-clay over the region, this feature and the absence of solid exposures can reasonably be attributed to a thick glacial accumulation; this may be morainic in origin and may be associated with the mass of ice which led to the formation of the Marrington Dingle overflow channel.
>
> In one field two wells have been dug near Whitepits and both provided glacial lake clays and some

boulder-clay; the depth of one well was 36 ft (11 m) and solid rock had not been reached. Trial holes dug to the north and south-west at Poundbank were also abortive, producing nothing other than boulder-clay. The delineation of the western boundary of the Ordovician is accordingly most inexact and the very fact that no feature is attributable to the Whittery Volcanic Group, which invariably is expressed in the topography, almost certainly shows the Ordovician is covered by glacial deposits almost as far as the Church Stoke – Chirbury road.

Classification of the Shelve Ordovician rocks

Lithostratigraphic subdivisions

The stratal subdivisions upon which Professor Whittard's map is based are lithostratigraphic units and represent the culmination of researches which began with Lapworth in 1887. The original terms were subsequently modified and expanded, particularly by Lapworth & Watts (1894, 1910), Lapworth (1916), Watts (1925) and finally Whittard (1931, and, to a lesser degree, 1940, 1955 and 1966). The manner in which the terminology evolved is shown by the comparative stratigraphical columns in Fig. 3. The stratigraphic terminology employed by Whittard and his predecessors does not conform with present-day requirements and does not follow the recommendations of either the Stratigraphic Committee of the Geological Society of London or the American Commission on Stratigraphic Nomenclature; consequently some appropriate modifications are proposed in the present paper. In an earlier publication, which contains his most detailed account of the Shelve Ordovician rocks (excluding the Habberley (now Shineton) Shales, of Tremadoc age), Whittard (1931) utilized a sequence of seventeen subdivisions, e.g. Mytton Flags, Aldress Shales, etc., which clearly correspond to what would nowadays be termed lithostratigraphic or rock-stratigraphic terms. Following Watts (1925 : 340) these were grouped into ten so-called 'Stages', an inappropriate method which utilized what is strictly a chronostratigraphic term for what were in fact groupings of lithostratigraphic subdivisions. These 'Stages' were then variously assigned to the 'Arenigian, Llanvirnian, Llandeilian and Caradocian', terms which in this form cannot be employed as Series of the Ordovician System. These last were replaced in the descriptive text of the same paper by the more appropriate usage of Arenig, Llanvirn, Llandeilo and Caradoc Series, though without comment. The same 'Beds' and 'Stages' were utilized in the 1948 (second) edition of the Geological Survey's handbook on the geology of the Welsh Borderland (Pocock & Whitehead 1948 : 42) but abandoned in the latest (third) edition of the same work by Earp & Hains (1971 : 41). Eventually Whittard (1952 : 156–165, table III) omitted all mention of the above 'Stages', while most of the lithostratigraphic terms of the 1931 paper were used and correlated with the various Series of the Ordovician, though the Hope Shales were shown as undivided.

In the first part of his Shelve trilobite monograph (Whittard 1955 : 5) the Tankerville Flags, previously regarded as the topmost of four subdivisions of the Mytton Flags that had fallen into disuse, re-entered the stratigraphical succession without comment as a separate subdivision between the Mytton Flags and the Hope Shales. The Tankerville Flags were clearly regarded by Whittard as meriting separate status as their trilobite fauna was listed by him later (1966 : 299) in the distribution tables for the monograph, but in the same work (1966 : 303) he pointed out that they could be distinguished in only a restricted part of the outcrop. The Tankerville Flags had obviously not proved a satisfactorily mappable unit and were not differentiated as such by Whittard on any of his 6 in to 1 mile field maps, where only the Mytton Flags occupy the position between Stiperstones Quartzite and Hope Shales.

For present purposes it has been deemed appropriate to divide the Shelve Ordovician (excluding Tremadoc) rocks into three Formations, names introduced by Lapworth, and subdivided in turn into members that correspond to the lithostratigraphic terms used by Whittard and earlier workers. As far as possible the type locality or stratotype for each member is listed and illustrated by extracts from Whittard's unpublished maps; additional data have been compiled from his manuscript notes and, where necessary, published papers. Among the unpublished notes was a proposed zonal sequence founded upon trilobites, the vertical distribution of which was shown in detail in Part 8 of the monograph (Whittard 1966 : 299–302), and this has been incorporated in

CARADOC DISTRICT	SHELVE INLIER		CHARACTERISTIC TRILOBITE	STAGE	SERIES	GRAPTOLITE ZONE
			ASHGILL SERIES NOT REPRESENTED IN SHROPSHIRE			Pleurograptus linearis Zone questionably present in Shropshire
Onny Shales or Onnia Beds	ABSENT		Onnia superba	ONNIAN	CARADOC	
			Onnia gracilis			Dicranograptus clingani
			Onnia? cobboldi			
Acton Scott Beds			Platylichas laxatus & Calyptaulax actonensis	ACTONIAN		
Cheney Longville Flags			Broeggerolithus transiens	MARSHBROOKIAN		Zones ill-defined
			Broeggerolithus longiceps	LONGVILLIAN		
Alternata Limestone						
Horderley Sandstone			Broeggerolithus globiceps & B. nicholsoni			
			Broeggerolithus soudleyensis	SOUDLEYAN		Diplograptus multidens
Glenburrell Beds	CHIRBURY FORMATION	Whittery Shale Mbr	Broeggerolithus broeggeri			
		Whittery Volcanic Mbr				
		Hagley Shale Mbr				
		Hagley Volcanic Mbr				
		Aldress Member				
			Broeggerolithus ulrichi	HARNAGIAN		
Smeathen Wood Beds & Harnage Shales			Salterolithus caractaci			
			Reuscholithus reuschi			
Coston Beds & Hoar Edge Grits		Spy Wood Member	Costonia ultima	COSTONIAN		
ABSENT	MIDDLETON FORMATION	Rorrington Member	Marrolithoides arcuatus & Spirantyx calvarina		LLANDEILO	Nemagraptus gracilis
		Meadowtown Member	Lloydolithus lloydi & Cryptolithus inopinatus			Glyptograptus teretiusculus
		Betton Member	Trinucleus acutofinalis & Bettonia		LLANVIRN	Didymograptus murchisoni
		Weston Member	Platycoryphe vulcani			
	SHELVE FORMATION	Stapeley Shale Mbr	Stapeleyella inconstans & Ampyx linleyensis			Didymograptus bifidus
		Stapeley Volcanic Mbr				
		Hope Member				
		Mytton Member	Bergamia rhodesi		ARENIG	Didymograptus hirundo
			ill-defined interval			Didymograptus extensus
			Myttonia confusa			
		Stiperstones Member	Neseuretus grandior			
			No fossils found			
Shineton Shales	Shineton Shales				TREMADOC	

Fig. 4 Table showing lithostratigraphic subdivisions for the Ordovician rocks of the Shelve Inlier and the Caradoc District of Salop, with the corresponding Series and Stages (where available). Since this paper was submitted, the name *Cryptolithus inopinatus* has been changed to *Whittardaspis inopinata*.

the correlation scheme for the Inlier shown in Fig. 4. The lithostratigraphic sequence given below is followed in the descriptive account of the Shelve Ordovician rocks.

Chirbury Formation	Whittery Shale Member	1000 ft+	(305 m+)
	Whittery Volcanic Member	300 ft	(91.5 m)
	Hagley Shale Member	*c.* 1000 ft	(305 m)
	Hagley Volcanic Member	350 ft	(107 m)
	Aldress Member	*c.* 1000 ft	(305 m)
	Spy Wood Member	300 ft	(91·5 m)
Middleton Formation	Rorrington Member	1000 ft	(305 ft)
	Meadowtown Member	*c.* 1300 ft	(396 m)
	Betton Member	600 ft	(183 m)
	Weston Member	3600 ft	(1100 m)
Shelve Formation	Stapeley Shale Member		
	Stapeley Volcanic Member		
	Hope Member	800 ft	(244 m)
	Mytton Member	*c.* 3000 ft	(914 m)
	Stiperstones Member	estd 400 ft	(122 m)

The Shineton Shales

These strata, cropping out along the Habberley Valley between the Stiperstones on the west and Pontesford Hill and The Longmynd on the east, were termed Shineton Shales by Callaway (1878 : 333) on the basis of their lithology and stratigraphical position. Later Lapworth (1916 : 37) introduced the term Habberley Shales for them, a name retained by Watts (1925 : 339) as there was then no faunal evidence available to prove their equivalence to the Shineton Shales. Palaeontological proof was subsequently provided by Stubblefield & Bulman (1927 : 116–118), whose faunal lists indicated a close correspondence with the strata of the Wrekin District. Whittard (1931 : 323, *et seqq.*) continued to use the term Habberley Shales in an account (1931 : 324, fig. 43) of an excavation, made in the vicinity of Granham's Moor Farm, near Habberley, which demonstrated what he described as an unconformity, marked by a 3 in (76 mm) band of conglomerate, at the base of the overlying Stiperstones Quartzite. In view of the correspondence of dip below and above the basal conglomerate of the Quartzite, the latter may perhaps be better regarded as disconformable rather than unconformable upon the Shineton Shales. A brief mention of this locality prior to excavation and a few notes of other localities constitute the only records of the Shineton Shales in the Whittard documents. A later account by Whitehead (*in* Pocock *et al.* 1938 : 72) thought it unnecessary to retain the name Habberley Shales and commented on Whittard's excavation to the effect that the Stiperstones Quartzite/Shineton Shales junction was conformable though 'not necessarily without a break in deposition'. In the first part of his monograph on the Shelve Ordovician trilobites Whittard (1955 : 5) continued to use the term Habberley Shales, but his last published note on the subject (1960 : 144) regarded them as synonymous with the Shineton Shales. Whether one should assign these Tremadoc strata to the Cambrian or the Ordovician is beyond the scope of the present work, in which the Shineton Shales are excluded from the Shelve Formation.

Lithostratigraphic description of the Shelve Ordovician rocks

Shelve Formation

FIRST USAGE. As Shelve Series, by Lapworth (1887 : 662), composed of the Stiper Group, Ladywell Group and Stapeley Volcanic Group, in ascending order. The succession was later modified by Lapworth (1916 : 37) to comprise Mytton Group, Hope Group and Stapeley Group, though the lower and upper limits of the Shelve Series remained unchanged.

TYPE LOCALITY. Presumably the vicinity of Shelve hamlet, but no type section was designated.

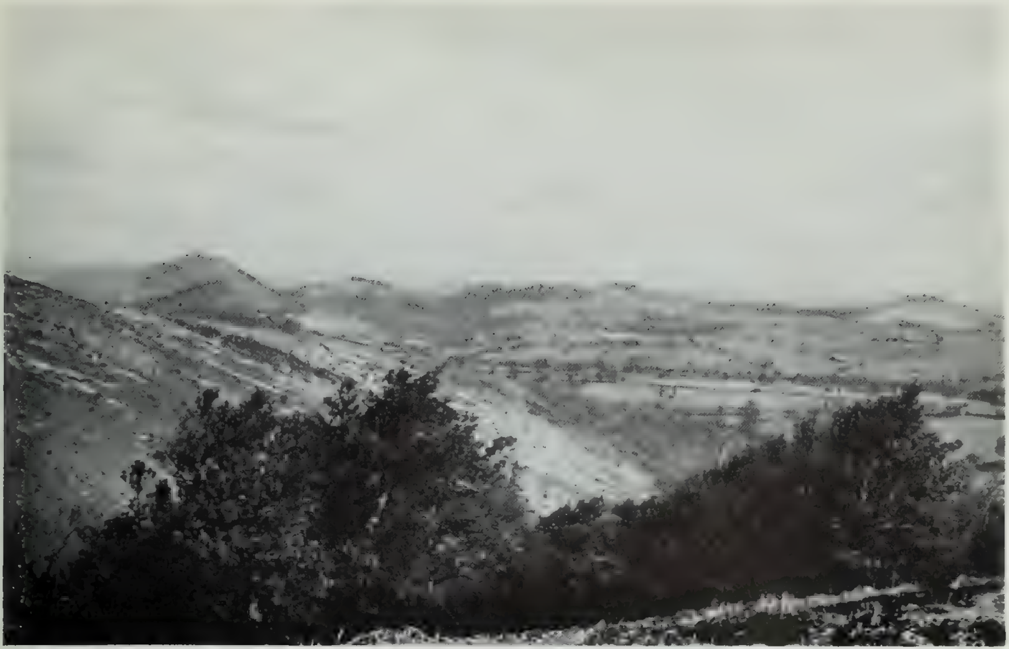

Fig. 5 Eastern margin of Shelve Inlier, showing Pontesford Hill (Western Uriconian) at left, and hills formed by Longmyndian rocks. View looking NE from above Upper Yessons, 0·9 mile (1·5 km) east of Snailbeach and situated on the outcrop of the Shineton or Habberley Shales.

Stiperstones Member

First usage. As Stiper Group, by Lapworth (1887 : 662), overlain by Ladywell Group. The original usage stated that the Group included 'the well-known Stiper Quartzites' and the term 'Stiper Stones (Quartzite)' was later listed by Lapworth & Watts (1894 : 317). Since then the name Stiperstones Quartzite has come into general use and is replaced by Stiperstones Member, though employed in the same sense.

Type locality. The escarpment of the Stiperstones, but no specific type section was designated.

Descriptive notes. Quartzites of the Stiperstones Member form a structurally complicated outcrop extending NE from the vicinity of the River Camlad, 1·5 km (0·94 mile) SE of Disgwylfa (Squilver) Hill in the south, over the Heath Mynd to Black Rhadley where it is crossed by an important oblique fault, beyond which minor faulting imposes a zig-zag outline upon the western boundary as far as The Bog. Here the outcrop is reintroduced on the northern side of another major oblique fault and runs through broken ground, each faulted mass tending to produce a crag, so typical of the Stiperstones and culminating in the Devil's Chair (Fig. 7). Succeeding to the NNE are Scattered Rock and Shepherd's Rock, beyond which the outcrop, though still faulted, is not so intensely shattered and jointed. The strata can now be followed northwards fairly readily, there being a significant change in strike north and south of Blakemoorgate, but near Granham's Moor an oblique fault, approaching the quartzite outcrop from the west, curves into the strike and by repetition of the beds creates an increased breadth of outcrop as far as just beyond Nill's Hill. North of here the breadth is once more reduced, the strike swings NE, and the outcrop terminates against the Coal Measures and glacial deposits of the Pontesbury district after having covered a distance of more than 10 miles (16 km).

The Stiperstones Member is composed of hard, resistant rocks and forms an eastern edge to the Shelve Inlier which attains a maximum height slightly in excess of 1725 ft (526 m). All along the escarpment the quartzite tends to weather into crags but nowhere is this type of topography

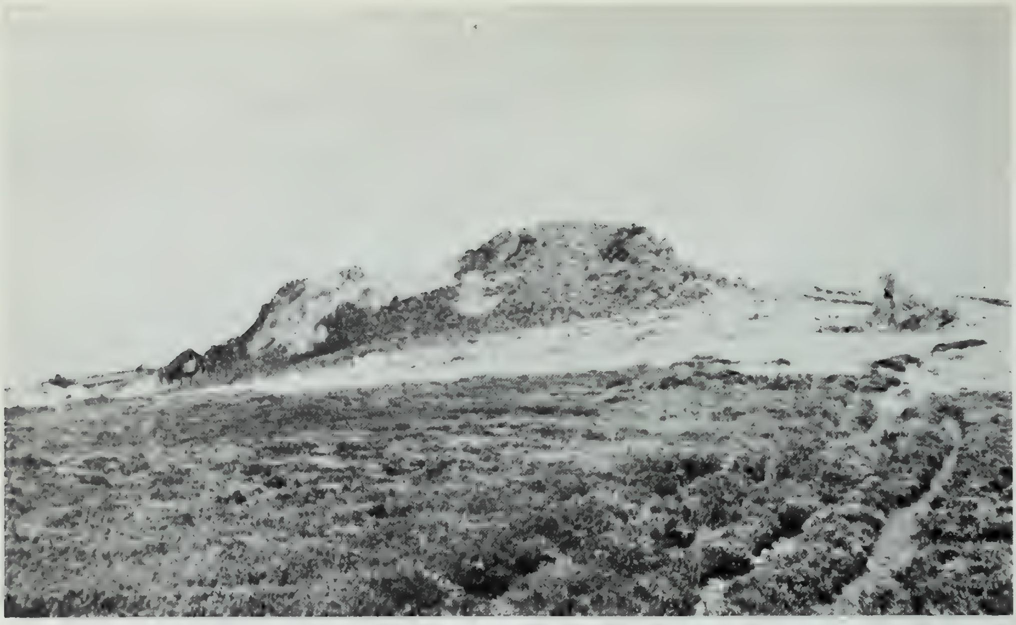

Fig. 6. Outcrops of Stiperstones (Quartzite) Member. View looking north from point south of Manstone Rock, between Devil's Chair and Cranberry Rock.

so well seen as between Cranberry Rock and the Paddocks, and The Rock and Nipstone Rock, which significantly are the two lengths where the outcrop shows the most complex fault-pattern.

Reliable figures for the thickness of the Stiperstones Member are difficult to determine. The angles of dip vary quickly and range from 40° to vertical, whilst in some places, as on both sides of the River West Onny and at Nill's Hill, the dip is reversed to the east. Nowhere is there a section through the Member, neither the upper nor the lower limit is visible in more than a few places, and only indirect evidence of the thickness can be utilized. Topography is a most uncertain guide because the escarpment is continually being degraded, crags are actively being reduced in height and enveloped in scree-clitter and, by virtue of bedding and of jointing parallel to the strike, rocks fall on both dip and scarp slopes. The marked change of slope on the scarp side suggests the outcrop of the softer Shineton (=Habberley) Shales, Tremadoc Series, but this can be deceptive because at several locations undoubted exposures of quartzite occur in what, on this assumption, should have been Tremadoc ground. Consequently the Stiperstones Member may at times be below the surface but farther down the scarp than is expected, and its failure to crop out is due to 'scaling-off' of the quartzites along the joints. On the dip slope, exposures are hardly ever seen owing to the blanket of quartzite blocks, heather and whinberry. How far west the top of the Member extends is frequently difficult to determine, and topography reveals little because the quartzites show a zone of gradation into the slightly less resistant Mytton Member. Thus the thickness of the Stiperstones Member as shown in the craggy exposures appears to be not more than 100 ft (30·5 m), which generally is probably correct because the crags are eroded from faulted blocks in which the top or bottom, or sometimes both boundaries, of the subdivision are cut out. The thickness of the Stiperstones Member probably does not exceed 550 ft (167·6 m) in the north of the inlier between The Paddock and Lord's Hill, but apparently increases SW to *c.* 650 ft (198 m) on the south side of Heath Mynd. The beds are probably strongly diachronic but palaeontological evidence is insufficient to prove this. The Member is invisible at the surface in the Shelve Anticline, but the estimated depth at which it has been supposed to occur is 1200 ft (366 m) (Hall 1919 : 12; Dines 1958 : fig. 2).

The dominant rocks of the subdivision are massive, compact and usually moderately well

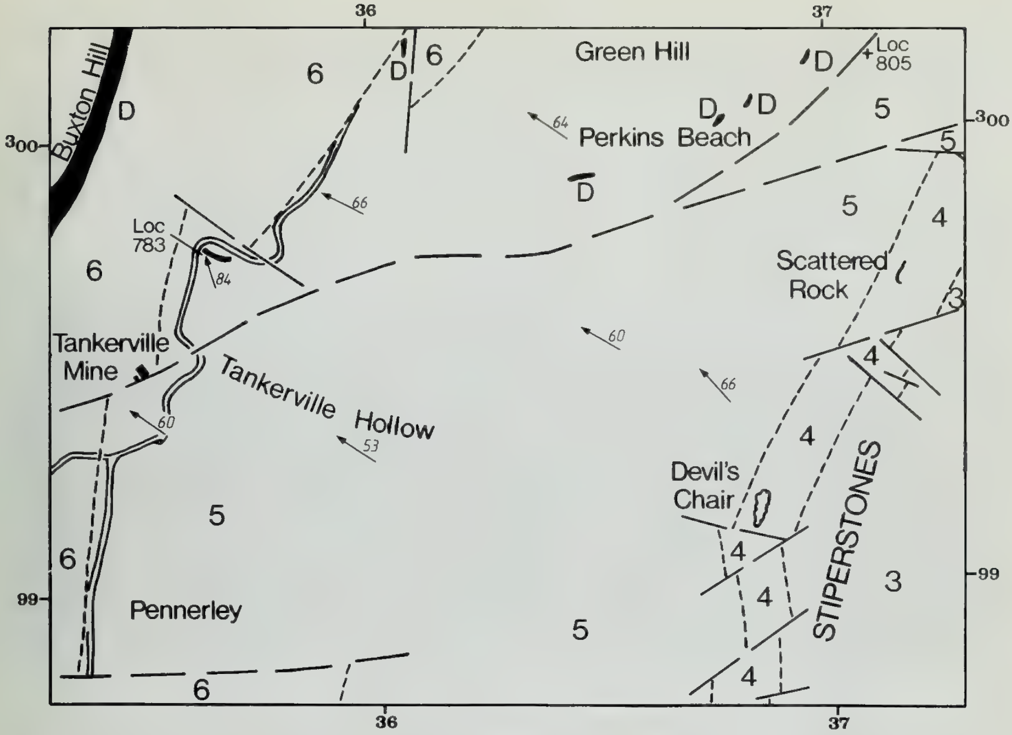

Fig. 7 Geological map of the area between Myttonsbeach and The Bog. Adjoins Fig. 10. 3 = Shineton Shales; 4 = Stiperstones Member; 5 = Mytton Member; 6 = Hope Member; black outcrop D = dolerite. (SO 39 and SJ 30)

bedded quartzites which are white, light grey, bluish-white or liver-coloured; they are sometimes colour-banded in alternations of bluish-grey and light fawn. The banding accentuates false bedding as seen on weathered joint faces, for example at the northern end of the Manstone Rock; occasionally the bedding is lenticular and produces lenses up to 2 ft (60 cm) long and a few cm thick; at other times it is undulose, the wavelength being 2–3 ft (about 75 cm) and the amplitude a few cm; symmetrical ripple-marks are uncommon, as in the Nill's Hill quarries. Hard, shiny, black bitumen was noted on joint faces north of The Hollies, Snailbeach and at Nill's Hill. Bedding surfaces show burial preservation examples of *Chondrites* sp., animal tracks referred to *Cruziana semiplicata* Salter (1866: 292) and fucoidal markings, but the commonest remains are worm-tubes infilled with sand which is coarser-grained than that of the surrounding quartzite. The tubes are at right angles to the bedding, frequently show paired openings as though they are U-shaped, and vary in diameter from $\frac{1}{8}$ to 1 in (3–25 mm). In regions where dips are high and the quartzites severely jointed, as at the Devil's Chair, the occurrence of these infilled worm-tubes is a distinct aid to the determination of bedding. Angular fragments of blue-black shale and sandy mudstones, as much as 2 in (5 cm) across and indistinguishable from the Mytton Member, lie in the bedding planes; they have often been removed from the quartzite by weathering, leaving characteristically-marked surfaces with flat-bottomed, vertical-sided, irregularly rectilinear depressions. Much of the compact quartzite is secondarily silicified and in extreme cases is converted into chert-like rocks; rarely the quartzites are felspathic.

The most frequently seen conglomerates are pale in colour, occur at any horizon, and are normally composed of a quartzite matrix in which small pebbles of quartz, chalcedony, quartz aggregate and cryptocrystalline felsite, rarely spherulitic, are included, and they seldom exceed 1 in (2·5 cm) in maximum diameter. Noteworthy is the absence of granite types and of feldspar,

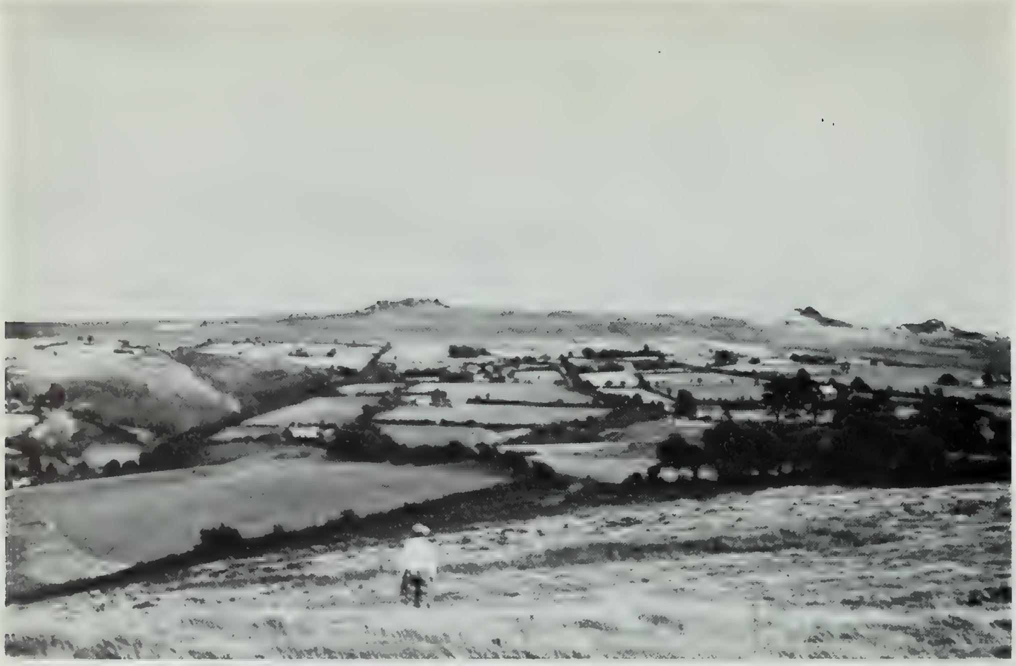

Fig. 8 View of the Stiperstones, with Tankerville Hollow on left, looking east from Round Hill, 0·7 mile (1·1 km) ENE of Shelve hamlet.

unless some of the fine-grained micaceous pebbles are highly weathered feldspar in which all traces of twinning are lost. The basal conglomerate, 3 in (7·5 cm) thick, exposed in an excavation by the side of a derelict concrete tank opposite Granham's Moor quarries, is much darker in colour owing to ferruginous and chloritic fragments, and interstitial argillaceous matter. The provenance of the conglomerates, and also of the quartzites, is unknown. If the derivation had been from the east, i.e. the direction of the immediate land-region of those times, the content of Uriconian and Longmyndian material would have been much higher than it is; consequently, an along-shore drift of sediment, presumably from the SW, is not unlikely. Also possibly bearing on this problem is the existence at Pontesford, only 1–2 miles (about 2·5 km) away, of representatives of the Caradoc Series which rest directly upon Pre-Cambrian. There are many geological anomalies here; the unconformity at Pontesford is undeniable yet there is no evidence of such an important hiatus in the corresponding succession of the Shelve Inlier. Important faults occur between the Inlier and the Ordovician outcrop of Pontesford, and two geological regions which were at one time widely separated may have been abruptly collocated by strike-slip faulting in which the movement was essentially horizontal, while downthrow may have brought to about the same present topographical level two deposition surfaces which originally were separated, relative to one another, by a large vertical interval.

The entire thickness of the Stiperstones Member is not, however, made up of quartzite and conglomerate. Towards the base are interbedded silvery, greenish-white, soft, soapy shales which have yielded dendroid graptolites and are only a few cm thick, whilst at Nills Hill thin papery shales and sandstones are present in bands up to 10 in (25 cm) thick. Elsewhere thin, micaceous, dark grey shales alternate with layers of coarse but friable quartzite, and these are included within massive quartzites. In the mid-thickness of the subdivision both soapy shales and fucoidal flags similar in lithology to the Mytton Member occur.

As revealed under the microscope, much of the compact quartzite has been secondarily silicified. Within narrow limits the grains are generally of uniform size and form an interlocking mosaic: the clear secondary silica has grown in optical continuity with the quartz of the original grains, which are frequently dusty from inclusions and are rounded, the ghost of their outlines being clearly evident in many samples. At other times, the original outline is lost and secondary silicification is then recognized by the irregular sutural contacts made between individual quartzite components. Secondary growth of silica does not usually form around quartz aggregates.

The normal sedimentary base of the Stiperstones Member has not been seen in any natural exposure, but the contact with the Shineton Shales was found to be exceedingly sharp in an excavation made some years ago near a disused concrete tank on the opposite side of the valley to the lower Granham's Moor Quarry. At its eastern extremity the excavation showed olive-green shales and micaceous flags; 5 ft (1·5 m) below the succeeding conglomerate Dr C. J. Stubblefield in 1931 collected *Shumardia pusilla* (Sars) and *Lingulella nicholsoni* Callaway, thus proving their Tremadoc age, *Shumardia pusilla* Zone (Whittard 1931 : 344). Resting upon, and inclined at the same angle as, these Shineton Shales is a 3 in (7·5 cm) band of dark, distinctive conglomerate which makes a clean-cut junction and is of a type unknown from the main mass of the Stiperstones Member. The conglomerate is succeeded by a thin band of broken shale, unlike the Shineton Shales, and finally by flaggy quartzites which definitely belong to the Stiperstones Member. The excavation was terminated by blocks of quartzite set in a sandy matrix, but these were not *in situ*. The junction between the Stiperstones Member and the Shineton Shales was taken at the base of the conglomerate because (i) no conglomerate is known in the Shropshire Tremadoc rocks; (ii) the conglomerate consists mainly of angular quartz grains, interstitial ferruginous and chloritic material, and rounded pebbles of quartz and quartz-aggregate, all of which can be matched in undoubted Stiperstone quartzite; and (iii) the Stiperstones Member is disconformable to the Shineton Shales as the younger of these Tremadoc deposits belong to the *Shumardia pusilla* Zone, whilst representatives of the higher *Apatokephalus serratus* Zone are absent. The disconformity can only be inferred on palaeontological and lithological evidence, because there is no discordance in angle of dip, neither is there any detectable difference in strike; but with such easily-deformed strata as make up the Shineton Shales, the mass of the overlying, thick Arenig beds has probably brought the inclination of their upper layers into coincidence with that of the quartzites.

The upper limit of the Stiperstones Member is different from the lower because there is no sharp line of demarcation; indeed, the condition is that found in passage beds where one lithology is superseded by another through a thickness of alternating types. Stratigraphically above the dominantly quartzitic beds is an interval, of unknown magnitude, wherein the light-coloured, secondarily silicified, clean quartzites alternate with striped, micaceous, rusty-weathering, bluish-grey shales and siltstones of an aspect like rocks found in the Mytton Member; these are included in the Stiperstones Member. Still higher, however, the clean quartzites are replaced by dirty, dark quartzites, usually but not always thin-bedded, carrying much argillaceous matter, alternating with sandy shales and flags; these are placed in the Mytton Member and clearly represent a sedimentary transition. Whereas the lower limit of the Stiperstones Member is precise, the upper can be drawn on the map only arbitrarily.

The commonest indications of organic life in the quartzite are innumerable worm-tubes of many sizes, 1 in (2·5 cm) and less in diameter, frequently but not always U-shaped, and filled with coarser-grained material than the enclosing sediment. Salter (1866 : 243, 256, 291–293, fig. 2; pl. 11B, fig. 27) compared the burrows with *Arenicolites linearis* (Hall). No corrugated skin has been detected in the many tubes which have been examined in the quartzites. The only other fossils are two pygidia of a large trilobite, *Neseuretus grandior* Whittard, and a sponge-spicule of which four axons are identifiable in thin-section. Until recently these were all the known fossils from the Stiperstones Member but now a few dendroid graptolites and some anomalous and structureless remains, which may be algal, have been recovered from silvery and soapy shales interbedded with quartzite in the quarry at the NW corner of Poles Coppice, north of Granham's Moor Farm. Unfortunately *Neseuretus grandior* and the dendroids are valueless for detailed correlation. *Neseuretus* is found in the Lower Ordovician, is particularly common in parts of the Mytton Member, and there is no reason to consider the Stiperstones Member to be other than Arenig in age.

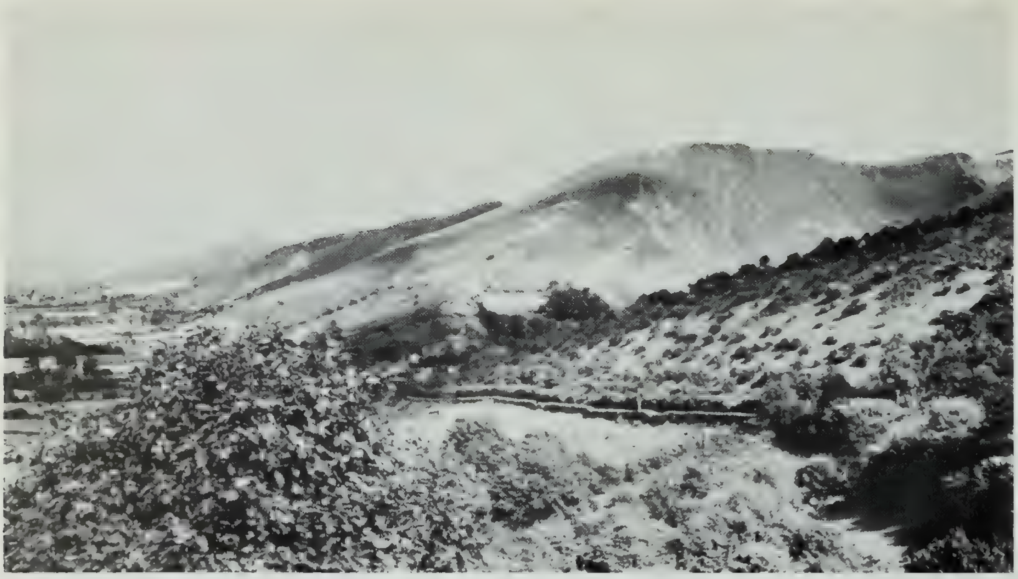

Fig. 9 Mytton Batch (= Myttonsbeach) and Snailsbeach, formed by rocks of the Mytton Member. View looking NNE from above Bergam, 1·3 miles (2·1 km) NNE of Shelve.

The quartzites accumulated as coarse-grained, worm-ridden sands with pebbly layers, and comprise a well-sorted deposit generally washed clean of mud. The fact that animal tracks were impressed and preserved suggests that the water was shallow and, indeed, the conditions may have been littoral. The sands were covered by muds for short intervals, particularly during the earlier periods of deposition, but mud and sandy mud became dominant towards the top of the subdivision as Mytton Member conditions became established.

Mytton Member

Type locality. Mytton Batch, near Snailbeach (Whittard 1960 : 194).

First usage. As Mytton Group, by Lapworth & Watts (1894 : 316), later renamed Mytton Flags by Lapworth & Watts (1910 : 752). The term Mytton Group as employed later by Lapworth (1916 : 37) was equivalent to the Stiper Quartzite and Mytton Flags of previous accounts; it was subsequently renamed Mytton Stage by Watts (1925 : 341), a term employed temporarily by Whittard (1931 : 323), and is now no longer used. Whittard's (1931 : 323, 325) usage of Mytton Flags corresponds to the present Mytton Member. He noted also Lapworth's subdivision of the unit into the following:

4. Tankerville Flags
3. Shelve Church Beds
2. Ladywell & Snailbeach Grits and Flags
1. Lord's Hill Beds.

The lowest of these was said to be unfossiliferous but brief notes were given on the faunas of the other three. Later Whittard (1940 : 154; 1952 : 157, table on p. 165; 1953 : 239, 240) used Mytton Flags in a similar sense without further subdivision and, noting Lapworth's thickness of 1600 ft (490 m) as being far too small, gave a figure of *c*. 3000 ft (915 m). He appears to have been uncertain how to treat the problem of further subdivision because in the first part of his trilobite monograph (1955 : 5) he reverted to the fourfold subdivision of Mytton Flags. In Part 8 of the same monograph, his final published contribution to the subject (1966 : 299–304), he rejected the term Shelve Church Beds (and presumably also the Lord's Hill, Ladywell and Snailbeach Beds) but retained the Tankerville Flags as a subdivision between the Mytton Flags and the Hope

Shales, though acknowledging that the distinctive lithology (comprising *c*. 100 ft (30·5 m) of 'bluish-grey flaggy shales with but little content of arenaceous material') and fauna could be recognized 'only over a restricted part of the outcrop'. The field mapping completed by Whittard shows only undivided Mytton Flags (now Mytton Member of the Shelve Formation), and nowhere was a separate Tankerville unit mapped. Consequently it is preferred to disregard the latter for most practical purposes although, in view of Whittard's 1966 remarks, the topic is discussed further with reference to the Tankerville area.

DESCRIPTIVE NOTES. Whittard (1931 : 325; 1960 : 194) noted the rocks only briefly as rusty-weathering, olive-green, ribbed, flaggy, sometimes quartzitic siltstones and bluish-grey, flaggy shales with a total thickness of *c*. 3000 ft (915 m). Lapworth & Watts' map (*in* Pocock & Whitehead 1948 : pl. 11) showed 'Mytton Flags & Shales' occupying two large outcrops within the Shelve Inlier: an elongated area NW of the Stiperstones and forming part of the eastern limb of the Ritton Castle Syncline and a subelliptical area centred approximately on the Shelve District and forming the core of the Shelve Anticline. This distribution corresponds broadly to the one shown in the present work.

In general the rocks of the Mytton Member comprise rusty-weathering, massive and flaggy, grey-green and blue-black siltstones and subsidiary shales. Although less resistant to erosion than the quartzites of the Stiperstones Member, the beds are generally more resistant than the shales of the succeeding Hope Member and form the conspicuous area of high ground extending from mid-way between Pontesbury and Minsterley SSW to Pennerley, beyond which the outcrop narrows markedly at the marshy area of The Bog. As Whittard (1931 : 325) emphasized, the rocks of the Mytton Member are important in that they contain the majority of the principal mineral veins (galena, blende, barytes) of the district and the remains of old workings are commonplace over much of the outcrop. Mining in the Shelve Inlier has since been reviewed in some detail by Dines (1958), who demonstrated that fault fissures receptive to mineral deposition are better developed in 'harder' formations such as the flags of the Mytton Member and die out in shales, where the veins are barren. The quartzites of the Stiperstones Member, although a hard formation, contain virtually no mineral deposits but the latter are common in rocks of the Mytton Member owing to the sealing effect of the overlying shales of the Hope Member, which prevented the upwards migration of mineral-bearing solutions. In the relatively few cases where mineralizing solutions escaped through the Hope Member shales to higher stratigraphic horizons in the Stapeley Volcanic and Hagley Volcanic Members, the occurrences are of barytes with only a few traces of galena and blende.

The striking unwooded valleys which drain the west side of the high ground underlain by the Stiperstones and Mytton Members are known locally as 'batches' or 'beaches'. They are remarkable physiographic features and in the case of Mytton Batch, usually written as Myttonsbeach on present-day maps, the slope of the head of the valley, covered by heather and whinberry, is 35°. Whittard's notes speculate that although it has been suggested that some of the batches are due to marginal overflows formed during the glacial period, they may in fact have originated from springs of which the flow passed down into the much lower-lying country occupied by the regressive Hope Member. If the difference in level was maintained between country formed of Mytton Member and that made of Hope Member, the velocity of the stream would be high and would give it considerable power to cut back quickly. The batches do not show devious courses – they are almost straight.

Mytton Batch, type locality for the Mytton Member, is a valley (Fig. 10) running east–west on the north side of Green Hill, some 3 miles (4·8 km) SSW of Minsterley. The rocks are particularly well exposed along the north side of the batch forming the south flank of Oak Hill. Those exposed in the section between the Minsterley – Pennerley road, near the one-time Stiperstones Inn, and the area east of Myttonsbeach cover the greater part of the succession, but the lowest strata are not visible and the first exposures recorded there are at MS Locs 832, where massive, brecciated siltstone, veined with quartz, is seen, and 831, where the rocks dip 46° at 315° true. The latter locality shows massive siltstones which in no way resemble shales, and this type of lithology is found elsewhere, including the heads of the batches, e.g. Tankerville Hollow (see p. 13). Generally

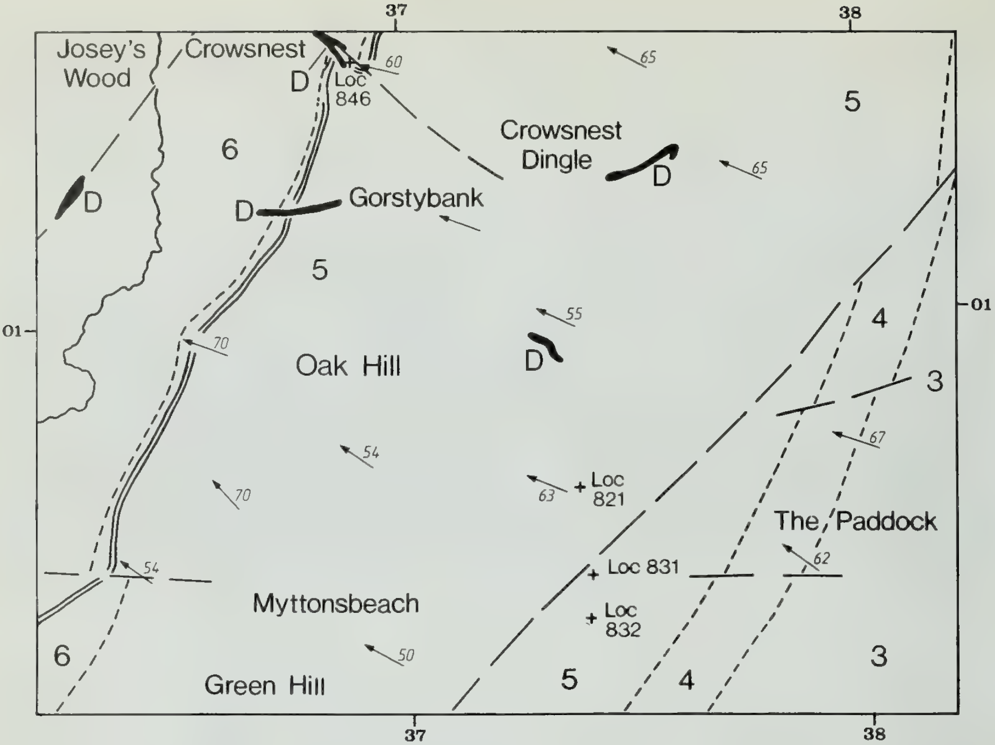

Fig. 10 Geological map of the Mytton Member at and north of the type locality. Adjoins Figs 7, 11. 3=Shineton Shales; 4=Stiperstones Member; 5=Mytton Member; 6=Hope Member; black outcrop D=dolerite. (SJ 30)

speaking, the softer siltstones and shales, particularly at the top and near the base of the Mytton Member, have proved fossiliferous, but the middle part of the succession, constituting the greatest thickness, comprises coarse siltstones, some of them very massive, and fossils are rarely found therein. From here westwards, there are numerous exposures in the area just east of the head of Myttonsbeach, including fossiliferous flags (Loc. 821) with *Myttonia confusa* Whittard, *Neseuretus* and *Ogygiocaris selwynii* (Salter), but these end at the valley, though the section continues along the top of its northern slope. Very massive flags make the main edge-feature of Mytton Batch, coarse siltstones of a type encountered in many places throughout much of the thickness of the Mytton Member. Looking downhill along the strike of these rocks, one can see three distinct ridges separated by hollows, features which indicate the alternation of hard and softer rocks. A similar alternation is applicable to most of the thickness of the Member as seen elsewhere in the district. Not only is there a coarse alternation involving thicknesses of up to 100–200 ft (30·5–61 m), but also within these thicknesses there are minor hard and soft strata alternating and in this respect the rocks of the Mytton Member are not unlike those of the Weston Member (see p. 38). This, however, is not the condition of the lowest beds, which are usually softer, silvery-grey weathering and frequently fossiliferous. The latter are the so-called 'Lord's Hill Beds' of Lapworth, and if we exclude these and the softer strata of the 'Tankerville Flags' from the total thickness, we are left with by far the greatest proportion of the Mytton Member made up of more massive rocks which presumably are Lapworth's 'Ladywell and Snailbeach Grits'.

On the south side of Green Hill the valley called Perkins Beach (Fig. 7, p. 13) contains numerous exposures of the Mytton Member, though the section is less extensive than that of Myttonsbeach. Loc. 805, beside an old adit, is important as it has yielded what is apparently the oldest fauna known from the Member, comprising *M. confusa*, *O. selwynii* and *Neseuretus* preserved in silver-grey weathering, micaceous, silty shales and flags. An interesting feature of this area is the occurrence of doleritic intrusions, which appear at the surface in crags and then disappear uphill; when followed along their strike, their place is taken by Mytton rocks which are sometimes indurated, sometimes not. One has the impression that the dolerites have only been exposed by the excavation of the valley, without which it is doubtful whether they would have broken surface.

The manner in which the main thickness of the Mytton Member is made up largely of greyish-weathering, blue-hearted siltstones is evident when working along Perkins Beach and the valley known as Tankerville Hollow, which runs ESE from Tankerville Mine (Fig. 7). The name Tankerville, incidentally, derives from an old term for an oven-pipe or organ-pipe, and refers to the shape of some of the mine shafts, which were narrower at the base than at the top. The alternation of predominant siltstones, which are usually exposed but yield few fossils, with shales, which may be fossiliferous but are rarely exposed, has made it impossible to subdivide the strata of the Mytton Member on the basis of their faunal content.

Bergam Quarry (Loc. 783), sited *c.* 1000 ft (305 m) NNE of Tankerville Mine and excavated in the highest portion of the Mytton Member (Fig. 7), is of interest as being the first locality at which species common to this horizon and the succeeding Hope Member were discovered. The rocks are bluish-grey, micaceous, flaggy shales with but little content of arenaceous material, and are hardened by a dolerite intrusion some 14 ft (4·3 m) wide. The shales on the north side of the intrusion are pale grey through a width of 11 ft (3·4 m), but those on the south side are not visibly altered. Fossils are hard to come by nowadays, but in the past the locality has yielded *Didymograptus hirundo* and numerous trilobites including *Bergamia rhodesi* Whittard, *Ectillaenus*, *Geragnostus*, *Placoparia* and *Pricyclopyge*.

To the south of Tankerville Hollow exposures of Mytton Member become fewer and an east–west fault running through Pennerley Mine (see Fig. 7) offsets the outcrop eastwards adjacent to the swampy area of The Bog. In the vicinity of The Bog lead mine no rocks are now visible *in situ*, though the tip heaps are composed of Mytton Member débris, but *c.* 1000 ft (305 m) to the ENE Loc. 279 yielded a single example of *Ogygiocaris* and a dubious *Tetragraptus*.

The outcrop of the Mytton Member narrows markedly to the south of The Bog and, accompanied by an elongated series of small faulted 'blocks' of Stiperstones Member, runs in a narrow strip bounded by two convergent faults which meet just south of the River West Onny and east of Cefn Gunthly (Map). From there to its termination about half a mile (0·8 km) east of Snead the outcrop is not well exposed and the western boundary is faulted against rocks of the Hope Member. The rocks are seen only intermittently on the heath-covered ground in the vicinity of Heath Mynd, and make up the eastern part of the hill feature of Roveries Wood, to the south of which they are overlain unconformably by Lower Silurian beds.

Turning to the area north of Myttonsbeach, the valley of Crowsnest Dingle shows numerous exposures of the more massive siltstone beds but, again, these die out eastwards so that the lowest strata of the Member are not exposed. Half a mile (0·8 km) farther NE the area east of Snailbeach (Fig. 11) is more informative. Immediately west of the mapped base of the Mytton Member is a building called Eastridge, just west of which, at Loc. 858, are exposures of typical flags with a preponderance of much harder layers of quartzitic rock. It is evident that the beds represent a transition from those of the Stiperstones Member, and similar strata follow successively to the west where, at Loc. 860, apparently the youngest beds of this sequence are still quartzitic and include a band 7 ft (2·13 m) thick. Whittard clearly contemplated separating these unfossiliferous, transitional rocks under the name Eastridge Beds, but their outcrop was shown only sketchily in the vicinity of Eastridge and he appears not to have recognized them elsewhere. In the same valley, however, and only a short distance south along the strike from Loc. 860, is an exposure (Loc. 158) of buff-weathering, bluish-grey hearted 'grits' which Whittard, in his notes, considered to be probably the 'Snailbeach Grits' of Lapworth. This conclusion seems arguable as the rocks occur below the shaly strata of Lordshill (see p. 18), and Lapworth (1916: 37) placed his 'Ladywell and Snailbeach Grits and Shales' above his 'Lord's Hill Beds'. However, to use either of these possibly synonymous terms, which cannot be employed with confidence outside a relatively restricted area, is to risk nomenclatorial confusion and it would be better to allow both to lapse.

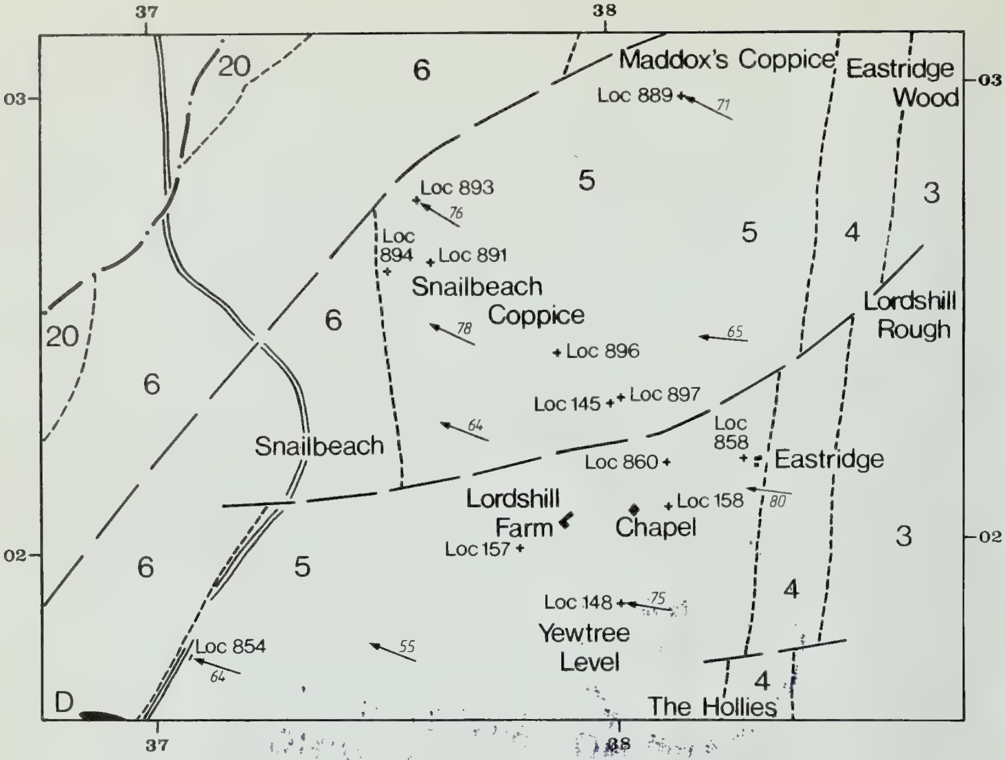
37
38
03
02
20
6
5
4
3
Maddox's Coppice
Eastridge Wood
Loc 889
71
Loc 893
76
Loc 894
Loc 891
Snailbeach Coppice
78
65
Loc 896
Loc 145
Loc 897
64
Snailbeach
Loc 858
Eastridge
Loc 860
Lordshill Rough
Lordshill Farm
Chapel
Loc 158
80
Loc 157
Loc 148
75
Yewtree Level
Loc 854
64
55
D
The Hollies

Fig. 11 Geological map of the area around Snailbeach. Adjoins Fig. 10. 3 = Shineton Shales; 4 = Stiperstones Member; 5 = Mytton Member; 6 = Hope Member; 20 = Silurian rocks; black outcrop D = dolerite. (SJ 30)

Although Whittard's notes state that the Lord's Hill Beds 'must not be confused with the fossiliferous beds of Lord's Hill so often mentioned by Salter', he appears to have used the terms in at least partly similar sense. South of the Baptist Chapel at Lordshill, towards Yew Tree Level, and to the north, in the vicinity of Perkins Level, shaly and occasionally flaggy beds overlie the transition beds noted above and have proved fossiliferous at a few places (Locs 145, 148, 897) along the strike; the fauna includes *Bergamia rhodesi*, *Myttonia confusa*, *Neseuretus parvifrons* (Salter), *Ogygiocaris selwynii* and *Redonia anglica* Salter.

Successively higher beds are encountered westwards along the road from Lordshill to Snailbeach and, to an even greater degree, NW from Perkins Level through Snailbeach Coppice. A dry, right-angled 'gutter' (Loc. 157), possibly a glacial overflow channel, centred *c.* 250 ft (76 m) west of Lordshill Farm, shows a large exposure in green-weathering, greyish, resistant, gritty flags. Across the valley and at a slightly higher horizon, a small pathside quarry (Loc. 896) *c.* 500 ft (150 m) NW of Perkins Level shows hard, blocky, jointed siltstones which are cut by a small dolerite intrusion immediately to the south. The beds here and in the adjacent spoil heap at one time yielded fossils including trinucleids, *Neseuretus* and *Ogygiocaris*. Other exposures (Fig. 11) in Snailbeach Coppice merit little detailed description but Loc. 891 shows massive quartzitic siltstones, while flags at Loc. 893 are disturbed by doleritic intrusions. The rocks at Loc. 894, a sunken cart-track, are apparently almost at the top of the Mytton Member but do not resemble the lithology of the 'Tankerville Flags' discussed earlier. A note here mentions that 'Tankerville Flags' were last seen in the roadside section (Loc. 846) just south of Crowsnest Dingle (Fig. 10, p. 18), but the field notes for that place mention only 'Mytton Flags'. The development of 'Tankerville Flags' in this area seems inadequately documented, though flags exposed by the side of the old railway at Loc. 854, *c.* 700 ft (210 m) NE of Crowsnest (Fig. 11), were described as

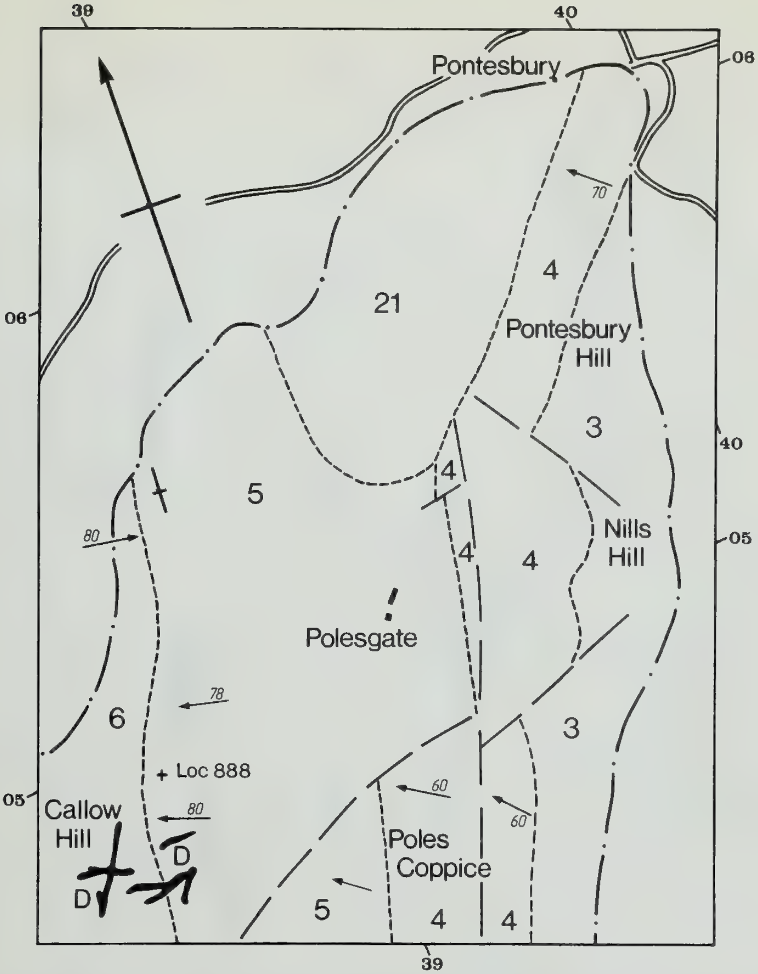

Fig. 12 Geological map of the area south of Pontesbury. 3 = Shineton Shales; 4 = Stiperstones Member; 5 = Mytton Member; 6 = Hope Member; 21 = Carboniferous rocks; black outcrop D = dolerite. (SJ 30)

'slightly more shaly than usual'. The wooded area of Maddox's Coppice, immediately NE of Snailbeach Coppice, contains few exposures but an old adit (Loc. 889) yielded fossils in silty shales and mudstones which occur at approximately the same horizon as similar strata near Perkins Level.

The Mytton Member's outcrop extends NNE (Fig. 12) to within about half a mile (0·8 km) of Pontesbury, where it is overlain unconformably by Carboniferous strata. Adjacent to the faulted western boundary is a large quarry (Loc. 888), excavated in the NE part of Callow Hill and approximately three-quarters of a mile (1·2 km) east of Minsterley. The rocks there are cut by dolerite intrusions which extend into the adjacent outcrop of the Hope Member; they show little variation and consist for the most part of massive, rusty-weathering, blue-grey siltstones which sometimes show thin, argillaceous layers and rod-like fucoidal structures.

All the outcrops of the Mytton Member so far considered form part of the eastern limb of the Ritton Castle Syncline. The remainder constitute an inlier, *c.* $2\frac{1}{2}$ by $\frac{1}{2}$ to $\frac{3}{4}$ mile (4 × *c.* 1 km) and elongated ENE, which forms the core of the Shelve Anticline. Truncated at its SW end by one of the Shelve Inlier's set of principal north–south tear-faults, the overall outcrop is divided into two

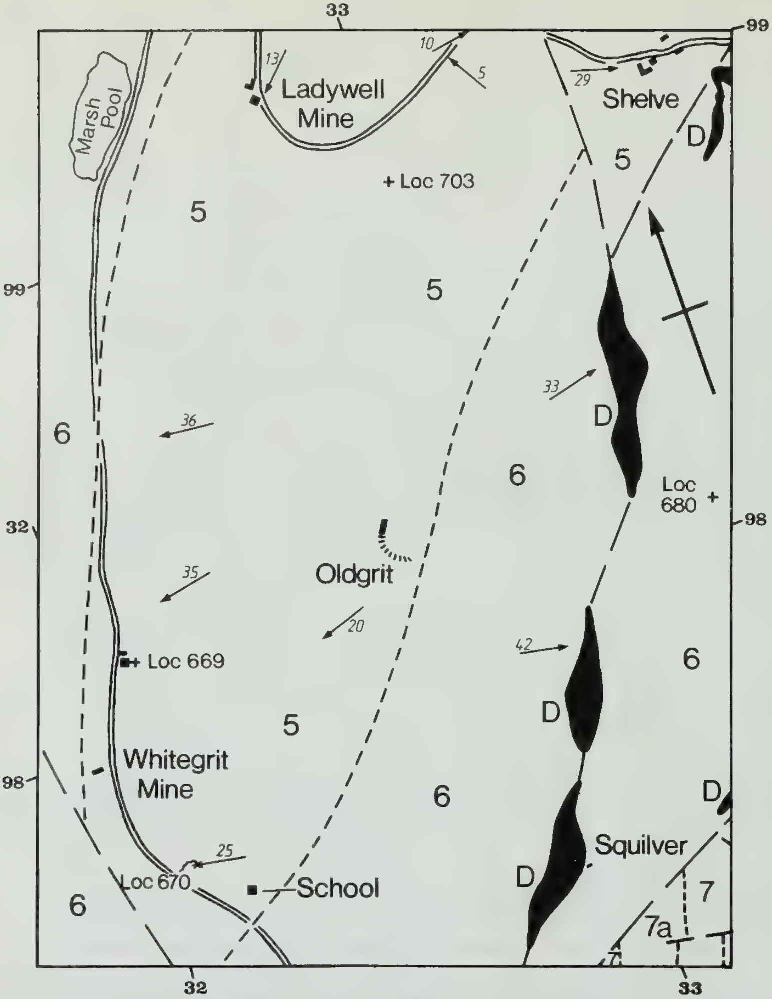
33
99
Marsh Pool
13
Ladywell Mine
10
5
29
Shelve
D
5
+ Loc 703
5
99
5
33
6
36
D
6
Loc 680 +
98
32
35
Oldgrit
20
42
6
+ Loc 669
D
5
Whitegrit Mine
98
6
D
25
Squilver
Loc 670
School
D
7
6
7a
32
33

Fig. 13 Geological map of the area SW of Shelve hamlet. Overlaps Fig. 14. 5 = Mytton Member; 6 = Hope Member; 7 = Stapeley Volcanic Member (7a = interbedded shales); black outcrop D = dolerite. (SO 39)

subequal parts by a second, subparallel fault which runs through Roman Mine and just west of Shelve hamlet. The SW part is centred broadly on Shelve Hill (Fig. 13), an elongated feature which stands notably higher than the surrounding, often badly-drained ground underlain by regressively-weathering shales of the Hope Member. Scattered exposures are most common towards either end of Shelve Hill, where three disused mines (Whitegrit, Oldgrit and Ladywell) are situated, but good sections are generally lacking. An old quarry (Loc. 670) 450 ft (137 m) NW of Whitegrit school exposes sandy, micaceous flags, weathering yellowish-grey, from which the type material of *Dictyonema cobboldi* Bulman (1928 : 33), together with *D. irregulare* Hall, was obtained. The locality was quoted by Whittard (1931 : 327) as being 330 yd (300 m) SSW of Whitegrit Mine, a misprint for SSE. About 450 ft (137 m) east of the same school, a collapsed mine shaft and its associated tip heaps of blue-hearted, shaly flags were noted by Whittard (1953 : 240) as having proved fossiliferous. The fauna includes *Ogygiocaris selwynii*, *Monobolina plumbea* (Salter), *Redonia anglica*, hyolithids and rare *Didymograptus*. In this area the linear arrangement of shafts and tip heaps running ENE between Whitegrit and Oldgrit suggests a

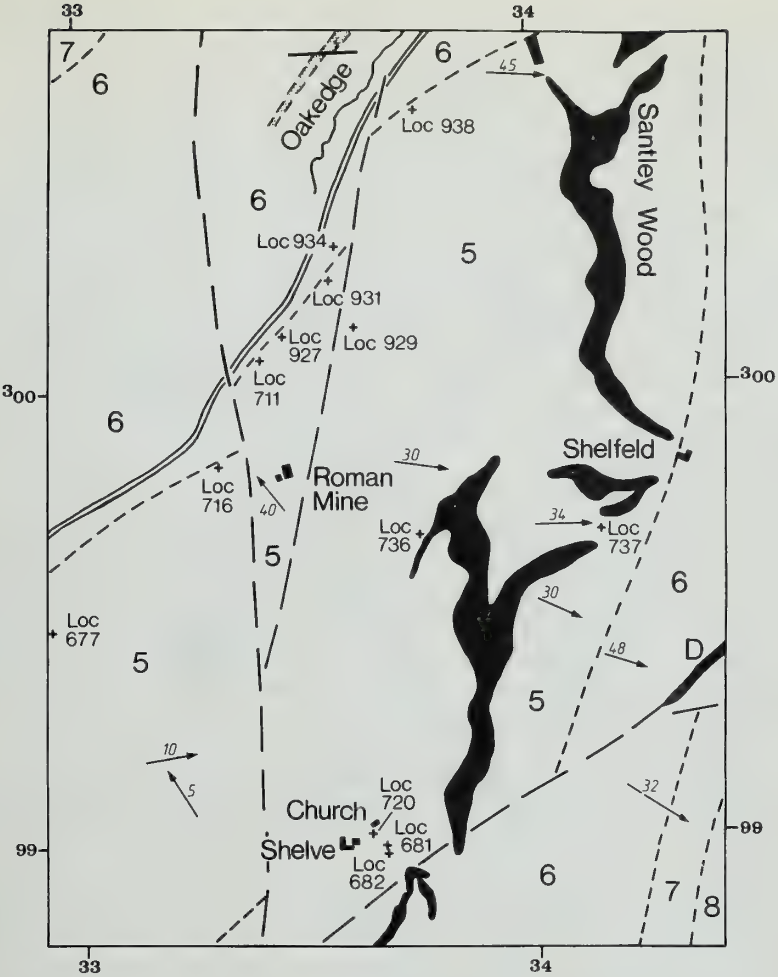
33
34
Oakedge
Santley Wood
Loc 938
Loc 934
Loc 931
Loc 927
Loc 929
Loc 711
Loc 716
Roman Mine
Loc 736
Shelfeld
Loc 737
Loc 677
Church
Shelve
Loc 720
Loc 681
Loc 682
D
5
6
7
8
45
30
40
34
30
48
10
5
32
300
99

Fig. 14 Geological map of the area north of Shelve hamlet. Overlaps Figs 13, 15, 16. 5 = Mytton Member; 6 = Hope Member, including 'chinastone' tuff bed (dotted); 7 = Stapeley Volcanic Member; 8 = Stapeley Shale Member; black outcrop D = dolerite. (SO 39, SJ 30)

line of at least brecciation if not faulting. In the same general area Loc. 669, 800 ft (244 m) at 034° true from Whitegrit school, produced only two specimens of possible ogyginid trilobites and a fragmentary graptolite, but the rocks are of interest as being softer than the typical lithology and probably lie very close to the top of the Mytton Member. At the NE end of Shelve Hill the rocks are not well exposed, and spoil heaps of shale (Locs 677, 703) in the vicinity of Ladywell Mine (Figs 13–14) nowadays provide the best opportunity for collecting fossils. The latter include *Ampyx salteri* Hicks, *Neseuretus*, *Ogygiocaris selwynii* and *Didymograptus*.

At the northern extremity of the SW half of the Mytton Member outcrop, beds very close to the boundary with the Hope Member are reported from the neighbourhood of Loc. 716, just west of Roman Mine (Fig. 14). As the hill is descended there appears to be an increase in shales approaching the condition of those forming the Hope Member and in this area there is thus at least a suggestion of a gradational boundary, a situation contrasting with that described in notes on part of the Hope Valley where a gradation was not definitely observed (see p. 24).

East of the north–south tear fault already noted as passing through Roman Mine, the NE half of the Mytton outcrop is roughly rhombic in outline, its SE boundary faulted against the

Hope Member. At Shelve hamlet the best-known rocks are those known at one time as Shelve Church Beds; they were once clearly exposed (Fig. 14) in the road beside All Saints Church but that outcrop is now much overgrown or built over and the beds are visible only in an adjacent field (Loc. 720). Excavation there exposed blue-black, shaly flags interleaved with silver-grey weathering, rusty-coated, blue-hearted shales in which the mainly graptolitic fossils occur matted together in thin bands. The fauna, though much quoted (for example by Whittard, 1931 : 326), has not received modern descriptive treatment but is famous for dendroids such as *Dendrograptus*, *Dictyonema* and *Desmograptus*, while graptolites including *Didymograptus extensus* (Hall) and *Glyptograptus dentatus* (Brongniart) also occur. Shelly fossils are in a distinct minority. Whittard's rejection of the term 'Shelve Church Beds' was noted earlier. In the relatively small area between Shelve Church and the faulted boundary against Hope Member to the SE, typical though unfossiliferous rocks of the Mytton Member were recorded at Loc. 681 (Fig. 14) while nearby, at Loc. 682, the 'Shelve Church Beds' lithology was seen, only a few metres from shales of the Hope Member which have been hardened by a dolerite intrusion. No other exposures of note occur in the immediate vicinity of Shelve but to the NE the outcrop is invaded by a large dolerite intrusion and metamorphosed 'flags' were at one time quarried at Locs 736 and 737, respectively WSW and SW of Shelfeld Farm.

From here to the NE apex of their subrhombic outcrop, the rocks of the Mytton Member are intruded by three additional masses of dolerite, the largest of which is elongated roughly north–south and underlies the western half of Santley Wood (Fig. 14). In the area immediately west of these intrusions the boundary between the Mytton and Hope Members is not actually visible but must lie near the base of the physiographic feature formed by the Mytton rocks near the SE side of Hope Valley and midway between Roman Mine and Hope village. Beds high in the Mytton Member were recorded at various points in the vicinity of an old quarry in dolerite, and Whittard's notes for his Loc. 938 state specifically that he had 'not definitely noticed any gradation in softness between Mytton Flags and Hope Shales'.

Between the two principal outcrops of Mytton Member in the Shelve district lies a small, triangular outcrop, bounded to east and west by faults which diverge northwards at an acute angle (Fig. 14). The area is of some interest as it contains numerous exposures and the remains of several workings including Roman Mine which, as the name suggests, was one of the original workings and dates from the second century (Dines 1958). A few typically Mytton fossils such as *Monobolina plumbea* and *Ogygiocaris selwynii* were found at Loc. 711 in micaceous, flaggy, blue-hearted shales which weather light grey. Beds in the highest part of the succession and almost immediately SE of the mapped upper boundary of the Mytton Member were seen at Loc. 927, where they include rocks said to resemble closely the 'Tankerville Flags' of the Stiperstones district, though the latter strata are generally regarded as not being developed in the Shelve district. Similar beds were seen also at Loc. 931. The rocks of the Mytton Member in this area were said to differ from the adjacent Hope Member in several respects: they are harder and more resistant, the contained mica flakes are usually larger, the bedding planes show flatter surfaces, and the edges of flaggy beds are angular and sharper. Spoil heaps (Loc. 934) of material taken from East Roman Gravels Mines, although composed of blue-black flags from the Mytton Member, may cause confusion as they are located on the mapped outcrop of Hope Member. Loc. 929, a short distance to the east, is of interest as it exposes strata of a lithology resembling that at Shelve Church, though no comparable graptoloids have been found. Whittard (1966 : 303) noted the occurrence of this apparently impersistent facies, which he considered to be probably older than that at Shelve, and advocated the rejection of Shelve Church Beds as a stratigraphical subdivision.

Hope Member

FIRST USAGE. As Hope Shales or Hope Shale Group by Lapworth & Watts (1894 : 316, 317), underlain by Mytton Group and overlain by Stapeley Ashes, a usage approximating apparently to that in the present paper. Lapworth's (1916 : 36) subdivision of the rocks into Lower, Middle and Upper Hope Shales did not pass into general usage.

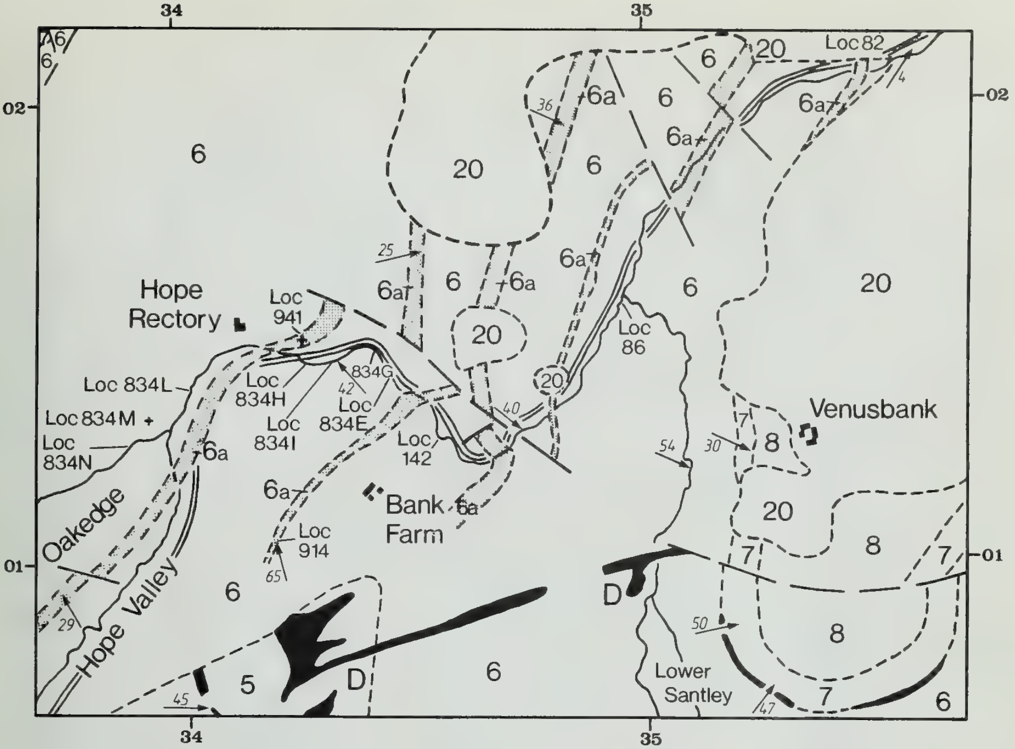

Fig. 15 Geological map of the Hope Valley. Overlaps Figs 14, 16. 5=Mytton Member; 6=Hope Member, including 'chinastone' tuff beds (dotted); 7=Stapeley Volcanic Member; 8=Stapeley Shale Member; 20=Silurian rocks; black outcrop D=dolerite. (SJ 30)

TYPE LOCALITY. Hope Valley, near Minsterley (Whittard 1960 : 156), where according to an earlier paper 'practically the whole thickness can be examined' (Whittard 1931 : 327).

DESCRIPTIVE NOTES. Whittard (1931 : 327, 328) described the rocks as comprising nearly 800 ft (244 m) of blue-black, rusty-weathering shales containing bands of so-called 'Chinastone Ash', volcanic horizons noted later by him (1960: 156) as 'occasional bands of andesitic tuffs'. The rocks were said to be recognizable only in the Shelve Inlier and were correlated with the *Didymograptus bifidus* Zone of the Llanvirn Series.

Outcrops of the Hope Member are the most extensive of all the subdivisions of the Shelve Ordovician succession, but the rocks weather regressively so that good exposures are not common and the beds often underlie areas of boggy, poorly-drained ground. Their role in the mineralization of the Inlier was noted earlier. The most important outcrops are those of the type area in the Hope Valley (Fig. 15) where the succession includes bands of andesitic tuffs at several levels. Blyth (1938: 397) pointed out that 'dust-tuff' is a more appropriate term for these extremely fine-grained tuffaceous horizons, which have proved locally useful in demonstrating the form of the Shelve Anticline (Whittard 1931*a* : 340). The subject had apparently not been considered in detail by Whittard at the time of his death, and for the present account it is preferred to retain, in spite of its admitted imperfections, the name 'chinastone', which is strongly entrenched in accounts of west Salop geology.

The Mytton/Hope Member boundary near the SE side of Hope Valley was noted earlier and exposures in this area are few, but at Loc. 914 the southern extremity of a thin bed of shattered 'chinastone' was seen to be interbedded with blue, micaceous shales. A section in blue-black shales stratigraphically below this tuff horizon is exposed in the bed of the stream flowing

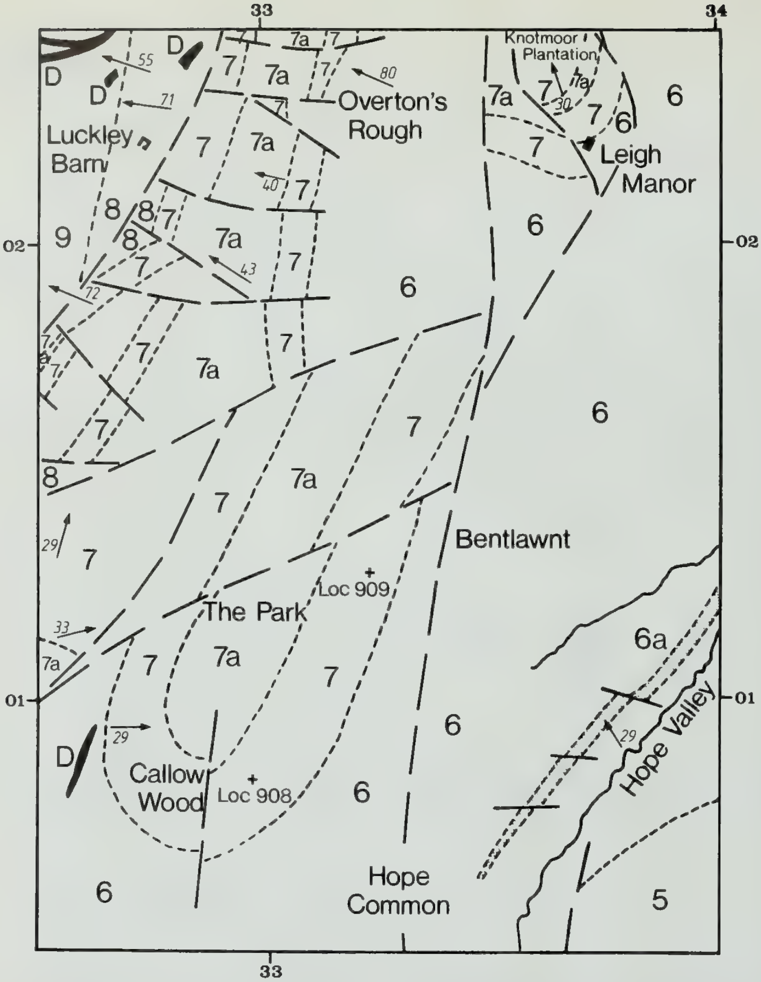
33
34
02
01
Knotmoor Plantation
Overton's Rough
Luckley Barn
Leigh Manor
Bentlawnt
Loc 909
The Park
Callow Wood
Loc 908
Hope Common
Hope Valley
D
5
6
6a
7
7a
8
9
55
71
80
40
43
72
30
29
33

Fig. 16 Geological map of the area between Hope and Overton's Rough. Overlaps Figs 14, 15, 17, 27. 5 = Mytton Member; 6 = Hope Member, including 'chinastone' tuff beds (dotted); 7 = Stapeley Volcanic Member (7a = interbedded shales); 8 = Stapeley Shale Member; 9 = Weston Member; black outcrop D = dolerite. (ST 30)

through Hope Valley *c.* 1500 ft (457 m) SSE of Hope Rectory, where Loc. 142 yielded *Pricyclopyge* and pendent didymograptids (Fig. 15). Farther upstream, shales above the same 'chinastone' are seen in a fairly long section which extends through most of the beds up to the next, and best-known, tuff horizon; fossils, including *Ectillaenus hughesi* (Hicks), *Pricyclopyge binodosa* and *Placoparia*, were found at Locs 834E, G, H and I.

The 'chinastones' have been found with certainty only in the vicinity of Hope hamlet, where there are two major bands (and also smaller, unimportant ones) around the NE-plunging nose of the Shelve Anticline. The first, and higher, band occurs as the faulted backbone of Oakedge (Figs 15–16) and continues down and across the valley to the disused roadside quarry (Loc. 941) adjacent to Ash Cottage and sited 450 ft (137 m) ESE of Hope Rectory. This is the often-visited, so-called 'Contorted Ash Quarry' (see Whittard 1931 : 328) in which the rocks are predominantly bluish-grey, exceptionally fine-grained tuffs with occasional subsidiary bands of shale. From the quarry, the outcrop extends northwards where it is first faulted and eventually ends against the outcrop of unconformable Silurian rocks. The second, lower band is thinner than the first and can be traced in the ridge NW of Bank Farm, into Hope Valley and thence up the northern flank where it makes a pronounced feature which apparently underlies unconformable Silurian strata forming an outlier in the vicinity of the 900 ft (274 m) contour. Both bands of 'chinastone' appear to wedge out to the SW and the upper one also thins to the NE. The large number of exposures of the 'chinastones' clearly indicates that the angle and direction of dip of these rocks are so variable that readings are of only general significance. The quarry near Ash Cottage gives a good impression of the structural condition of the 'chinastones', and their contortions and fracturings are probably a reflection of the structural complication of the shales which contain them. Thin-bedded competent rocks such as these behave as incompetent strata when contained in easily deformed beds such as shales, and the angles and direction of dips in shales of the Hope Member are unquestionably complex. It is thought that the latter rocks behaved as plastic material during the folding of the Shelve Anticline, but the deformation is better indicated by the 'chinastones' as their readings are less prone to modification by hill-creep than are the shales.

Successively higher horizons in shales overlying the upper 'chinastone' are encountered upstream along Hope Brook and the tributary stream running into it from the WSW (Fig. 15, p. 25). Several exposures, including Locs 834L, M and N, are recorded, yielding occasional trilobites (*Barrandia*) and graptolites, and displaying great variation of dip and strike. Downstream from Hope one encounters the succession of shales and 'chinastones' forming part of the southeastern limb of the Shelve Anticline. Fosiliferous shales in Hope Brook at Loc. 86 and the unconformable Ordovician/Silurian junction at Hope Quarry (Loc. 82) were noted by Whittard (1958 : 11).

From Hope Valley the outcrop of the Hope Member extends northwards in a broad strip until it terminates beneath Recent deposits just north of the Brockton – Minsterley road (B.4499). The outcrop (Fig. 17) is cut by conspicuous dolerite intrusions which are irregularly elongated ENE. Exposures are generally uncommon but both the igneous rocks and shales with occasional flags are seen in a stream valley which runs north almost along the centre of the outcrop, where Locs 57–60 yielded trilobites and graptolites.

South-west from Hope Valley, a large outcrop is mapped along the NW flank of Shelve Hill, forming part of the western limb of the Shelve anticline and flooring the poorly-drained areas of Black Marsh and The Marsh. Along the SE side of the Mytton outcrop in the Shelve area, a narrower outcrop of Hope Member forms part of the eastern limb of the anticline, and débris from an old mining level (Loc. 680 – see Fig. 13, p. 22) 300 ft (90 m) north of Shelve Pool yielded a few fossils including *Illaenopsis* and *Pricyclopyge*. The two limbs of the anticline converge to form a single, wide outcrop near the well-known eminence of Corndon Hill, the geology of which was described by Blyth (1944 : 178; pl. 20) whose boundaries for the dolerite phacolith were incorporated by Whittard in the present geological map.

Beyond Corndon, several minor intrusions (Map) of dolerite occur as well as the larger mass of the Cwm Mawr picrite (Fig. 19) described in detail by Blyth (1944 : 187). Apart from the igneous rocks, the most notable place-name in this area is Brithdir farm (Locs 635, 640) where shales of the Hope Member at one time yielded numerous fossils, some of which were illustrated in Whittard's trilobite monograph. The outcrop of the Hope Member terminates at the Silurian unconformity midway between Church Stoke and Snead, but shales were seen in the stream sections at and SW of Llanerch (Locs 603, 605 and 609; Fig. 19) and a few typical fossils were found.

About a mile (1·6 km) ESE of Llanerch lie the southernmost outcrops of the Hope Member in the eastern limb of the Ritton Castle syncline. The rocks, generally poorly exposed, are intruded by the elongated doleritic mass of Disgwylfa (now Squilver) Hill, described by Blyth (1944 : 171) and termed originally the Pitcholds intrusion, after a farm sited farther east and on the outcrop of Mytton Member. Disturbed shales in the highest part of the Member were seen just west of The Hollies farm (Fig. 20) but from there, NE along the strike, the strata are little in evidence, though an old trial shaft in the vicinity of the River West Onny produced a tip-heap (Loc. 254, Fig. 21, p. 32) of poorly fossiliferous, slightly hardened shales.

Beyond the river a narrow strip of Hope Member extends NE alongside the feature formed by the Stiperstones and Mytton Members as far as the south side of The Bog, where the outcrop

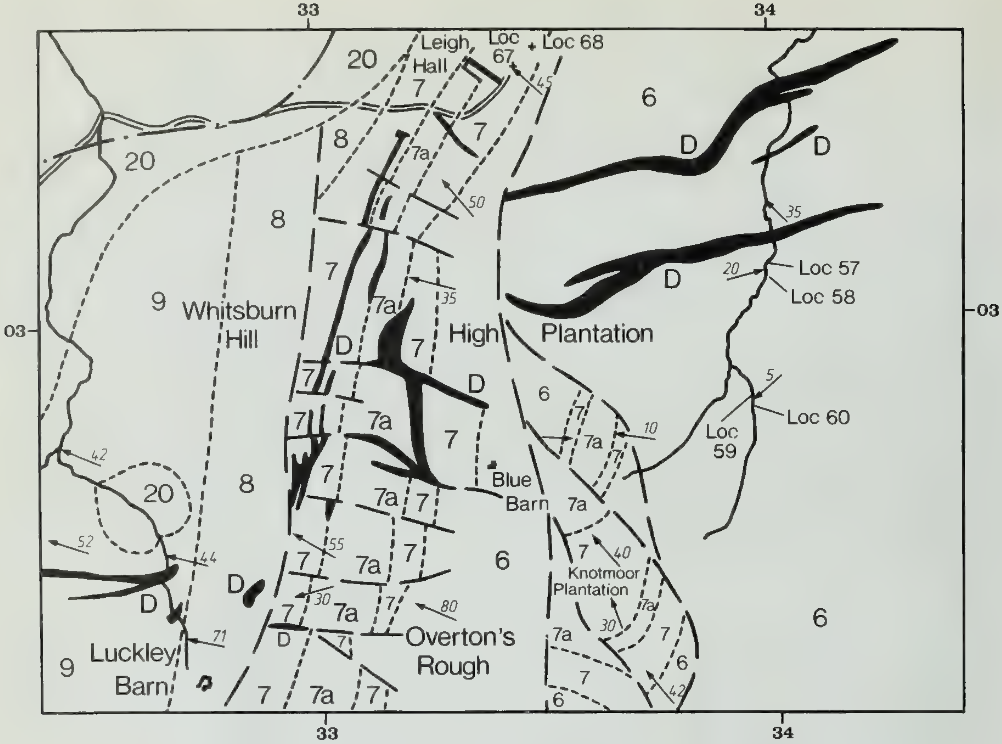

Fig. 17 Geological map of the area between Leigh Manor and Leigh Hall. Overlaps Figs 15, 16, 17. 6 = Hope Member; 7 = Stapeley Volcanic Member (7a = interbedded shales); 8 = Stapeley Shale Member; 9 = Weston Member; 20 = Silurian rocks; black outcrop D = dolerite. (SJ 30)

suddenly widens and is bounded on its SW side by a fault which cuts out the Stapeley Volcanic and Shale Members. Most of the vicinity of The Bog lacks exposures but a stream flowing west and SW near Ritton Farm and Ritton Castle (Fig. 22, p. 33) shows several exposures of shales, flags and occasional tuffs finally mapped by Whittard as Hope Member, though his notes at one time attributed them to the Stapeley Volcanic Member.

The outcrop around The Bog and, immediately to the north, Pennerley (Map) is shown as being cut medially by an almost north–south fault which then curves slightly NNE coincident with the elongated dolerite intrusion of Buxton Hill (Fig. 7, p. 13) and is intersected by another fault extending from Shelve hamlet NE to Maddox's Coppice (Map and Fig. 11). North-east from Buxton Hill an elongated outcrop has been mapped along the eastern limb of the Ritton Castle syncline, but the junction with the subjacent Mytton Member is not well exposed, though outcrops of the latter are relatively abundant to the east. A quarter of a mile (0·4 km) west of Crowsnest, a stream runs north through Josey's Wood (see Fig. 10, p. 18) and eventually joins Hope Valley Brook. Just SE of the point where the stream cuts the unconformable Silurian rocks (Map), massive, blue-black shales of the Hope Member exposed in the stream valley produced graptolites and trilobites (mostly *Pricyclopyge binodosa* (Salter) but occasionally *Corrugatagnostus* and *Stapeleyella*), a fauna considered at one time by Whittard (1931 : 327) to be especially characteristic of what were then termed 'Lower Hope Shales', a term now superseded.

Little of note was recorded from the remaining outcrop, which extends for about another two miles (3·2 km) before it disappears beneath Recent deposits at a point half a mile (0·8 km) east of Minsterley. The rocks are much obscured by glacial deposits, which attain a thickness of 20 ft (6 m) in a stream section 2000 ft (600 m) NW of Maddox's Coppice, but reappear along the line of the disused Snailbeach railway as it nears Callow Hill (Fig. 12, p. 21), a locality noted

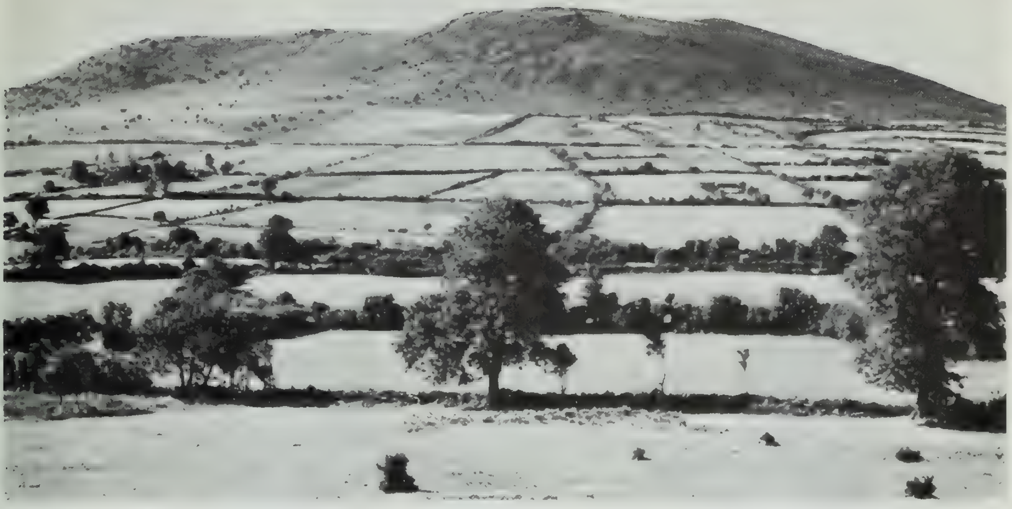

Fig. 18 Corndon Hill, 3 miles (4·8 km) ESE of Chirbury, formed by a resistant dolerite phacolith intruded into regressive Hope (Shale) Member. View looking SW from Squilver.

earlier in connection with rocks of the Mytton Member quarried close by. Doleritic intrusions cut the Mytton rocks just south of the quarry but most of them form a complex area within the outcrop of the Hope Member.

Stapeley Volcanic Member

First usage. By Lapworth (1887 : 662) as Stapeley Volcanic Group, the topmost of three subdivisions of his Stiper Group (Fig. 3, p. 6). In this original usage the term corresponded apparently to the combined Stapeley Volcanic and Stapeley Shale Members of the present paper. The separation and use of the terms Stapeley Volcanics and Stapeley Shales dates from Whittard (1931 : 329), but the latter strata had been differentiated earlier, as Upper Stapeley Shales (now superseded), by Lapworth (1916 : 37). This last work recognized the existence within what is now the Stapeley Volcanic Member of a sequence of three volcanic horizons, separated by 'Lower Shales' and 'Middle Shales'. For these volcanics the names Lower (Hyssington) Ash, Middle (Tashkar) Ash and Upper (Todleth) Ash were introduced, but they did not pass into general use.

Type locality. Stapeley Hill, near Minsterley, according to Whittard (1960 : 254).

Descriptive notes. Rocks of the Stapeley Volcanic Member crop out along the western limb of the Shelve Anticline and are even more extensively developed in both limbs of the Ritton Castle Syncline. The former area includes the type area of Stapeley Hill, 1¼ mile (2 km) SE of Rorrington, where a single group of shales separates a lower and an upper set of volcanics, each of which is intruded by a dolerite sill (Map). The succession there dips approximately NW at from 54° to 66° and much of the ground is not well exposed, but mapping of even small faults is facilitated by the features formed by the resistant volcanic rocks.

In the area SW of Stapeley Hill the shales and upper set of volcanics are intruded by the NE extension of the large mass of andesite which forms the greater part of the hill Lan Fawr, three-quarters of a mile (1·2 km) west of Corndon Hill. An additional much faulted area occupied by

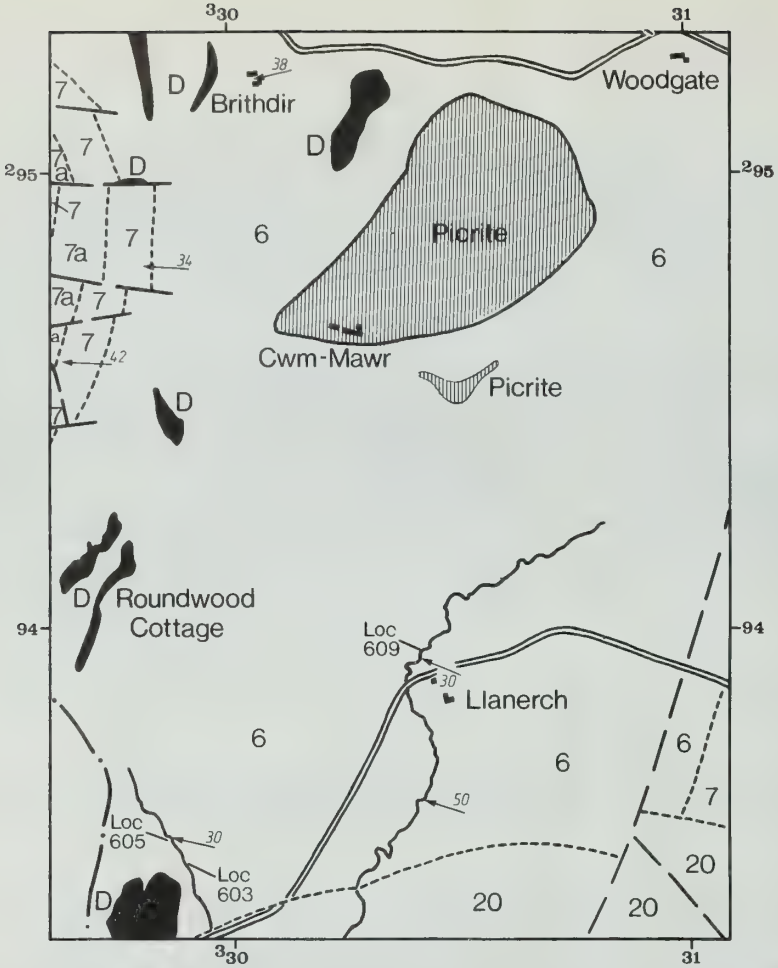

Fig. 19 Geological map of the area west of Hyssington and south of Corndon Hill. Overlaps Fig. 20. 6—Hope Member; 7=Stapeley Volcanic Member (7a=interbedded shales); 20—Silurian rocks; black outcrop D=dolerite; vertically shaded outcrops=Cwm-Mawr picrite. (SO 29, SO 39)

the Stapeley Volcanic Member extends south beyond Lan Fawr and another, slightly larger one runs south along the eastern flanks of the intrusive andesite masses of the hill called Roundton (sometimes written as The Roundtain) and Todleth Hill.

Faulting at the NE end of Stapeley Hill cuts out most of the Stapeley Volcanic Member until one reaches the vicinity of Bromlow Callow and The Park, about a mile (1·6 km) east of Meadowtown (Figs 16, 27, p. 40), where lithic tuffs (including Locs 908–9) are folded into a syncline, truncated to the north by a sigmoidal east–west fault which skirts the south side of Luckley Hill. From there the rocks of the Stapeley Volcanic Member form a strip-like outcrop, 'stepped' at intervals by small faults, which extends (Fig. 17, p. 28) to the northern boundary of the Inlier just north of Leigh Hall (not to be confused with Leigh Manor, a building situated 2620 ft (799 m) at 329° true from the Rectory at Hope). Whittard's map shows the succession within the Volcanic Member north of Luckley Hill to be similar to that of Stapeley Hill, that is with a single shale horizon separating two sets of volcanics. On the other hand at Luckley Hill itself, a fault-bounded area shows apparently a more complex sequence of two shales separating three volcanic horizons, the topmost one of which contains a further subsidiary bed of shale. The apparent incoming of

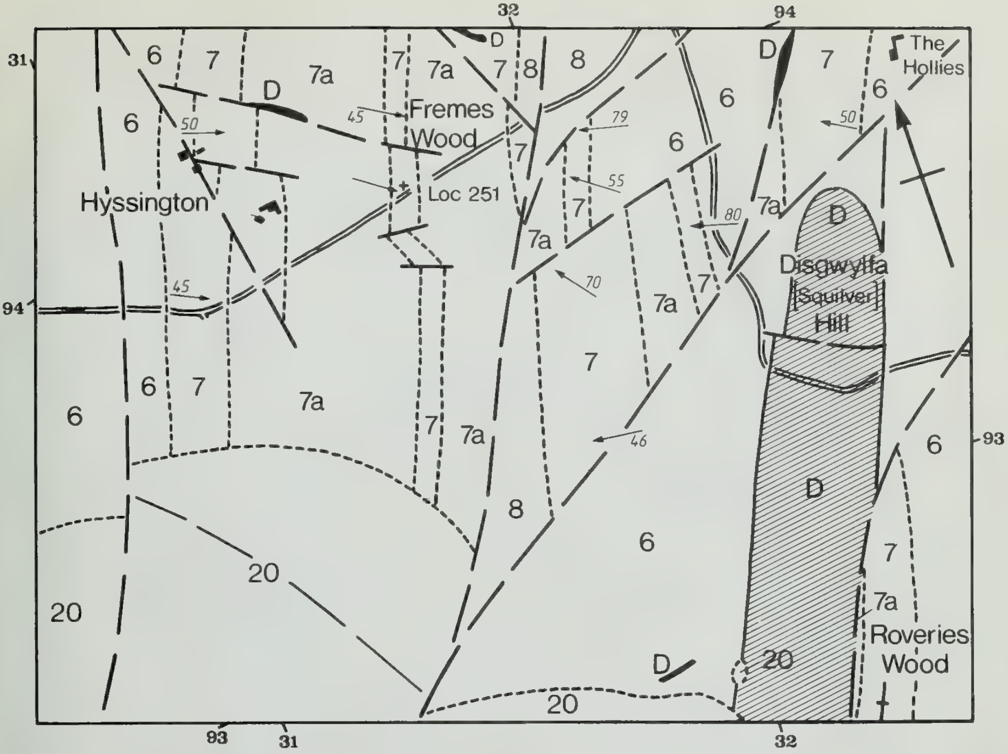

Fig. 20 Geological map of the area SE of Hyssington, in the SE part of the Shelve Inlier. Overlaps Fig. 19. 6 = Hope Member; 7 = Stapeley Volcanic Member (7a = interbedded shales); 8 = Stapeley Shale Member; 20 = Silurian rocks; black outcrop D = dolerite. Note particularly also the large dolerite of Disgwylfa (Squilver) Hill, shaded diagonally, and dips indicating the Ritton Castle Syncline. (SO 39)

another volcanic horizon coincides with a southerly widening of the mapped outcrop of the Volcanic Member. In the roadside section just east of Leigh Hall (Locs 67, 68) 'ashes' in the lower part of the Volcanic Member alternate rapidly with rusty-weathering, occasionally fossiliferous, blue-black shales (Fig. 17, p. 28). The evidence of the rocks indicates that the vulcanicity was submarine, probably in short, sudden bursts separated by periods of quiescence whose duration exceeded that of the vulcanicity, so that a benthic fauna could become established.

In the vicinity of Knotmoor Plantation, three-quarters of a mile (1·2 km) NE of Luckley Hill, is a fault-bounded series of outcrops of Stapeley Volcanic Member which according to Whittard's mapping probably include a sequence of at least two volcanic and two shale horizons, the possibility of any higher horizon having been eliminated by faulting (Map). An account by Blyth (1938), based on mapping and excavation of the section NW of Leigh Manor (Figs 16–17), gave an estimated thickness of 417 ft (127 m), made up of two pyroclastic divisions and an intervening group of shales with thin tuffs. Whittard's map shows a similar succession, but the upper pyroclastic rocks form a feature which is succeeded to the NW by a hollow from which the presence of, probably, another shale horizon is inferred. The relationships of the rocks in this complex area are not clear and the above interpretation must be regarded as tentative.

In the SE of the Shelve Inlier, the Stapeley Volcanic Member is encountered first in Roveries Wood, half a mile (0·8 km) NE of Snead (Fig. 20, above) where it forms an elongated, partly fault-bounded outcrop immediately adjacent to the well-known dolerite intrusion which extends NE to form Squilver Hill. The principal area of volcanics commences a short distance to the NW and can be traced to the NE as two parallel series of outcrops, separated by Stapeley Shale

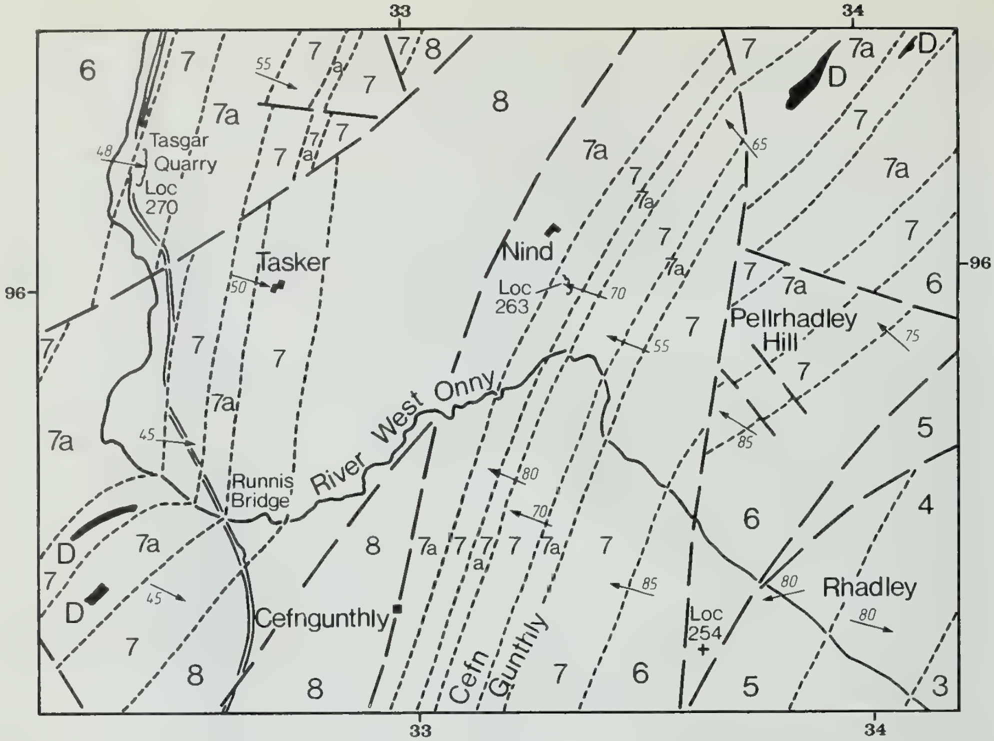

Fig. 21 Geological map of the valley of the River West Onny near Tasgar and Nind. Adjoins Fig. 22. Note dips showing the form of the Ritton Castle Syncline. 3 = Shineton Shales; 4 = Stiperstones Member; 5 = Mytton Member; 6 = Hope Member; 7 = Stapeley Volcanic Member (7a = interbedded shales); 8 = Stapeley Shale Member; black outcrop D = dolerite. (SO 39)

Member forming the core of the Ritton Castle Syncline. The dips of the volcanic rocks show clearly the form of the syncline, but the interbedded shales are less well exposed. Resistant features formed by the volcanics have aided the mapping of numerous faults, including north–south tears and complementary shears which are responsible for a gap in the continuity of the outcrop of the Stapeley Shale Member SE of Hyssington. In this area (Fig. 20) the SE-dipping succession comprises three volcanic horizons separated by shales. Several exposures of the lowest volcanics occur in the immediate vicinity of Hyssington, and rocks of the middle horizon were quarried (Loc. 251) at the south end of Fremes Wood, a quarter of a mile (0·4 km) east of the village, where both tuffs and interbedded shales were seen. Still farther NNE a similar sequence of three volcanic horizons was mapped beyond the valley of the River West Onny at Runnis Bridge, an area in which the most noteworthy locality (Fig. 21) is Tasgar (sometimes Tasker or, rarely, Tashkar) Quarry (Loc. 270), named for the nearby farm. The quarry, once well-known as a fossil locality but now practically worked out, is cut in massive tuffs of the Volcanic Member and the fossils came from subsidiary, interbedded shales.

At the southern end of the eastern limb of the Ritton Castle syncline a sequence of three volcanic horizons and two intervening sets of shales is not readily apparent at first owing to faulting near the north end of Squilver Hill. The sequence is demonstrable along the hill named Cefn Gunthly (or Cefn Gwynlle), 'stepped' at intervals by small transverse faults, and continues across the valley of the River West Onny. A third set of shales mapped at the top of the sequence beside the north end of Cefn Gunthly apparently was regarded as distinct from the Stapeley Shale Member, the outcrop of which is separated by a fault immediately to the west.

Just north of the West Onny, in Nind Wood and some 400 ft (122 m) SSE of Nind (sometimes

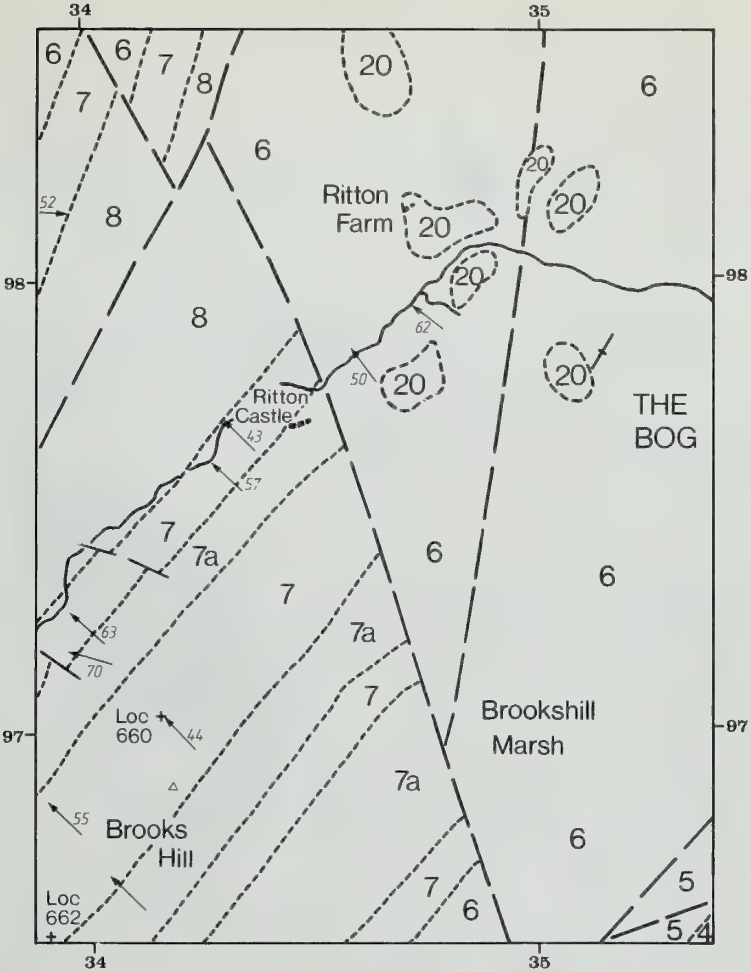

Fig. 22 Geological map of the synclinal area around Ritton Castle and The Bog. Adjoins Fig. 21. Note the small Silurian outliers. 4 = Stiperstones Member; 5 = Mytton Member; 6 = Hope Member; 7 = Stapeley Volcanic Member (7a = interbedded shales); 8 = Stapeley Shale Member; 20 = Silurian rocks. (SO 39)

Nynd or Neint) Farm, is Nind Quarry (Fig. 21, Loc. 263). The section, in the highest of the three volcanic horizons, shows tuffs which sometimes form large, nodular masses, weathering to a gingerbread colour, and may possibly have been calcareous. Interbedded shales at one time yielded numerous fossils, but collecting is not now profitable.

The volcanics of the Nind area are truncated a short distance to the east by one of the Inlier's conspicuous north–south tear-faults which runs between Cefn Gunthly and Black Radley Hill and skirts the western margin of Heath Mynd. Beyond the fault-line, at and near Brooks Hill, three-quarters of a mile (1·2 km) NE of Nind Quarry, Whittard's mapping (Fig. 22) shows the outcrop of the Stapeley Volcanic Member to be decidedly broader, with four volcanic horizons separated by shales. Even this appears to be a somewhat generalized picture and the notes on Loc. 660, 530 ft (162 m) at 348° true from the summit of Brooks Hill, emphasize the difficulty of distinguishing a detailed sequence of shale bands and tuffs in badly-exposed terrain. At this point the dip-slope of the Volcanic Member, instead of presenting a uniform appearance, exhibits two narrow 'benches' which can only be assumed to mark shaly horizons, though the

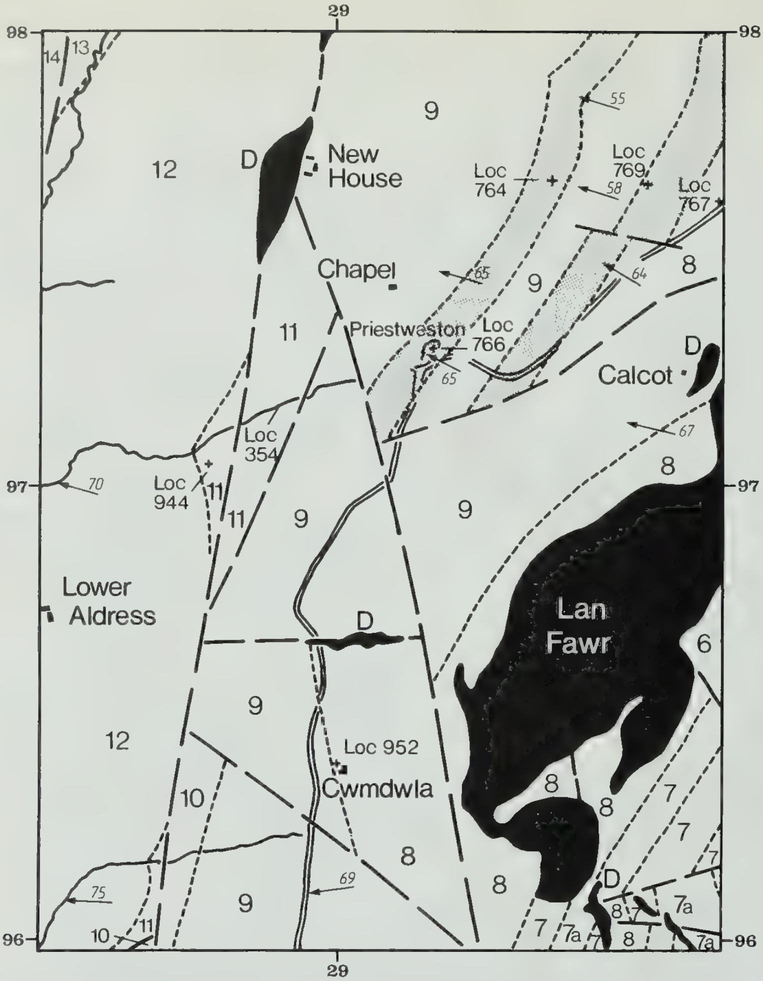
29
98
98
14
13
9
55
12
D
New House
Loc 764
Loc 769
58
Loc 767
Chapel
65
9
64
8
11
Priestweston
Loc 766
65
D
Calcot
67
Loc 354
97
70
Loc 944
11
11
9
9
8
97
Lower Aldress
D
Lan Fawr
6
9
12
Loc 952
Cwmdwla
10
8
8
7
7
7
8
69
75
9
8
D
7a
8
7
7a
7
7a
8
7a
96
10
11
96
29

Fig. 23 Geological map of the Priestweston area and the andesitic intrusion of Lan Fawr. Adjoins Fig. 24; overlaps Figs 30, 32. 7 = Stapeley Volcanic Member (7a = interbedded shales); 8 = Stapeley Shale Member; 9 = Weston Member, including 'grit' horizons (dotted); 10 = Betton Member; 11 = Meadowtown Member; 12 = Rorrington Member; 13 = Spy Wood Member; 14 = Aldress Member; black outcrop D = dolerite; main black outcrop = andesite. (SO 29)

hillside is bracken-covered and there is little evidence of rock except for widely dispersed blocks of tuff. The observation is recorded to emphasize the importance within the volcanics of shale bands which may range in thickness from several yards (metres) to 1–2 in (2·5–5 cm) in extreme cases. The note goes on to speculate that it may eventually prove necessary not to separate (what is now) the Stapeley Shale Member from the Volcanic Member, but no such action was ever taken by Whittard. Loc. 662, on the SW side of Brooks Hill and 1400 ft (427 m) at 217° true from the summit, is of particular interest as Whittard described the low, cliff-like section there as showing interbedded, coarse-grained lithic tuffs, crystal tuffs and ashy shale, varieties of rock which recalled the beds near Leigh Manor described in 1938 by Blyth (see p. 31). The wide outcrop of the Volcanic Member extends NE of Brooks Hill for another half mile (0·8 km) and is then truncated by a prominent NNW–SSE fault.

The Stapeley Volcanic Member in the western limb of the Ritton Castle syncline extends NE to a point half a mile (0·8 km) NE of Shelve hamlet. The outcrop is truncated by faulting but in addition the sequence is much attenuated and only a single volcanic horizon was mapped there, overlain by the Stapeley Shale Member. After a gap of 1460 yd (1·34 km) along the strike, the outcrop reappears in a small area NE of Lower Santley, SE of Hope. There also a single volcanic horizon was mapped, succeeded apparently by the Stapeley Shale Member (though poorly exposed and its outcrop largely inferred), the two subdivisions together being in the form of a small syncline, unconformably overlain by the Lower Silurian strata of the Venusbank district (Fig. 15, p. 25). In this area the map of Lapworth & Watts (*in* Pocock & Whitehead 1948 : pl. 11) shows a very large outcrop of Stapeley Volcanics on ground that is now known to be occupied largely by Silurian rocks.

Stapeley Shale Member

FIRST USAGE. As Upper Stapeley Shales, by Lapworth (1916 : 37). Subsequently modified to Stapeley Shales by Whittard (1931 : 323) and so used by him in later publications.

TYPE SECTION. Chosen by Whittard (1960 : 254), who described the beds as usually unfossiliferous; Holywell Brook, NW of Stapeley Hill and 1·75 miles (2·4 km) NNW of Shelve hamlet. Earlier Whittard (1952 : 159) noted an upward gradation from the Stapeley Shales into the Weston Beds at Holywell Burn (=Brook), so that an arbitrary boundary between the two had to be chosen.

DESCRIPTIVE NOTES. The strata of the Member are typically 'bluish-grey, rusty-weathering, soft shales' (Whittard 1931 : 330) and crop out within two elongated areas which form the western limb of the Shelve Anticline and the core of the Ritton Castle Syncline. Good continuous sections through the Shale Member are rare and even Holywell Brook, the type section, exhibits only the upper portion clearly, although the underlying Stapeley Volcanic Member crops out not far away (Fig. 25, p. 37). At this point Holywell Brook arises on the NW side of the north end of Stapeley Hill in an area of swampy ground with no solid outcrop, and it is not until the stream meets the west side of Valley Knoll that exposures of the Stapeley Shale Member are encountered. Here and in the stream section separating Valley Knoll from Rorrington Hill are seen strata interpreted as the highest of the Shale Member, dipping NNW at 50°–60° and succeeded by Weston Member. Whittard's arbitrary selection of the boundary has already been noted and was taken near the western end of an outcrop (Loc. 462) elongated east–west beside the northern bank of Holywell Brook, just west of its confluence with the tributary stream flowing from the SSE (Fig. 25, p. 37). At the western end of this outcrop were seen flaggy beds that could be assigned without much hesitation to the succeeding Weston Member, but farther east the rocks are more shaly with bands up to 2 in (5 cm) thick of micaceous shale resembling the typical lithology of the Stapeley Shale Member. The latter also show an anomalous increase of dip which is thought to be due to more than landslipping, and an almost continuous section (Loc. 463) along part of Holywell Brook farther east also exhibits variations in dip and strike. It is possible that such discrepancies may be the result of a fault running through the badly-exposed area of Rorrington Covert, and Whittard's notes show that he was considering an alternative interpretation which is shown in Fig. 26, p. 37. The lithological transition from Stapeley Shale Member to Weston Member is reflected to some degree in the type of fauna present; ogyginid trilobites are present in both subdivisions but the Weston Member contains a bivalve and lingulid brachiopod fauna which is almost unknown in the underlying Shale Member.

Some 1·62 miles (2·6 km) SSW of Holywell Burn, a road section (Loc. 767) NE of Priestweston (Fig. 23) cuts through part of the highest third of the Member and is of interest as it demonstrates the gradual appearance of more flagstone beds until the arbitrary base of the Weston Member is reached, in this instance at a point closer to Priestweston.

In the area between Priestweston and Holywell Brook the boundary of the Stapeley Volcanic and Shale Members runs NE along the edge of Stapeley Hill but is not generally visible. Of particular interest, therefore, is a section in the lower portion of the Shale Member at an old mining adit (Loc. 453) situated 2400 ft (732 m), 282° true from Stapeley Farm (Fig. 24). The beds of the Shale Member here are rusty-weathering, dark, bluish-grey shales, with occasional spheroidal concretions, and an apparently unfaulted thickness of 198 ft (60·35 m) was measured

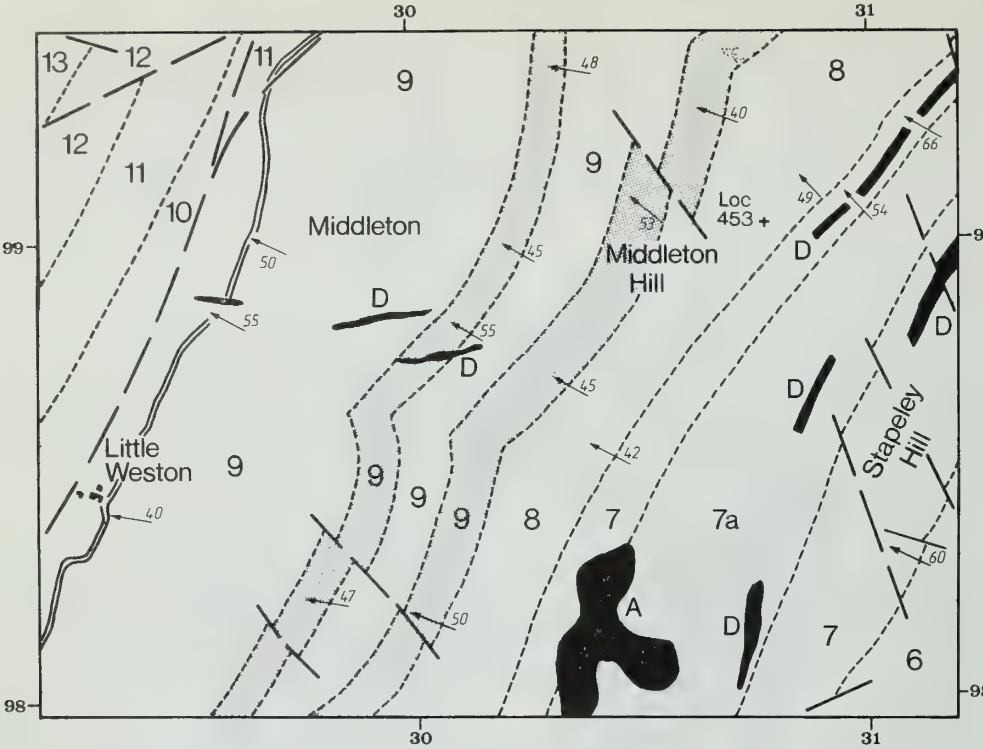

Fig. 24 Geological map of the area NE of Priestweston. Adjoins Fig. 23; overlaps Figs 25, 29. 6 = Hope Member; 7 = Stapeley Volcanic Member (7a = interbedded shales); 8 = Stapeley Shale Member; 9 = Weston Member, including 'grit' horizons (dotted); 10 = Betton Member; 11 = Meadowtown Member; 12 = Rorrington Member; 13 = Spy Wood Member; black outcrop D = dolerite; black outcrop A = andesite of Lan Fawr. (SO 29, SO 39)

along the adit. A normal contact with the underlying Volcanic Member was demonstrated by a junction bed 5 ft (1·52 m) thick, comprising an alternation of shales and tuffs and indicating a gradual passage between the two members.

Outcrops of the Stapeley Shale Member extend intermittently southwards from Priestweston for 2 miles (3·2 km) until they are terminated by glacial deposits just south of the village of Hurdley. An elongated hollow between Todleth Hill and Roundton (Map) has been mapped in part as a NW extension of the outcrops of Shale Member which run along the eastern margin of the intrusive masses of andesite. The rocks are exposed at various points along the northerly-trending stream NW of Hurdley and graptolites of 'tuning-fork' type were collected at Loc. 624. Exposures are poor along the eastern margin of Todleth Hill, but shales belonging to the Member were found in an excavation for a water-pipe near the north end of the hill.

Still forming part of the western limb of the Shelve Anticline, the outcrop of the Stapeley Shale Member extends NE for about 2½ miles (4 km) before ending beneath the unconformable cover of Lower Silurian strata which marks the northern boundary of the Shelve Inlier in the vicinity of Leigh Hall, a mile (0·6 km) south of Worthen (Fig. 17, p. 28). The outcrops in this structurally more complex area are discontinuous and the rocks are not well exposed.

In the eastern part of the Shelve Inlier, rocks of the Stapeley Shale Member form an elongated outcrop, often broken by faults, which extends ENE along the axis of the Ritton Castle Syncline from a point 0·62 mile (1 km) north of Snead (Map) for a distance of 4½ miles (7·24 km) to Round Hill, near Pennerley. The rocks are indifferently exposed and no noteworthy sections or localities are recorded. A further outcrop is largely inferred to the NW of Lower Santley, 0·42 mile (0·67 km)

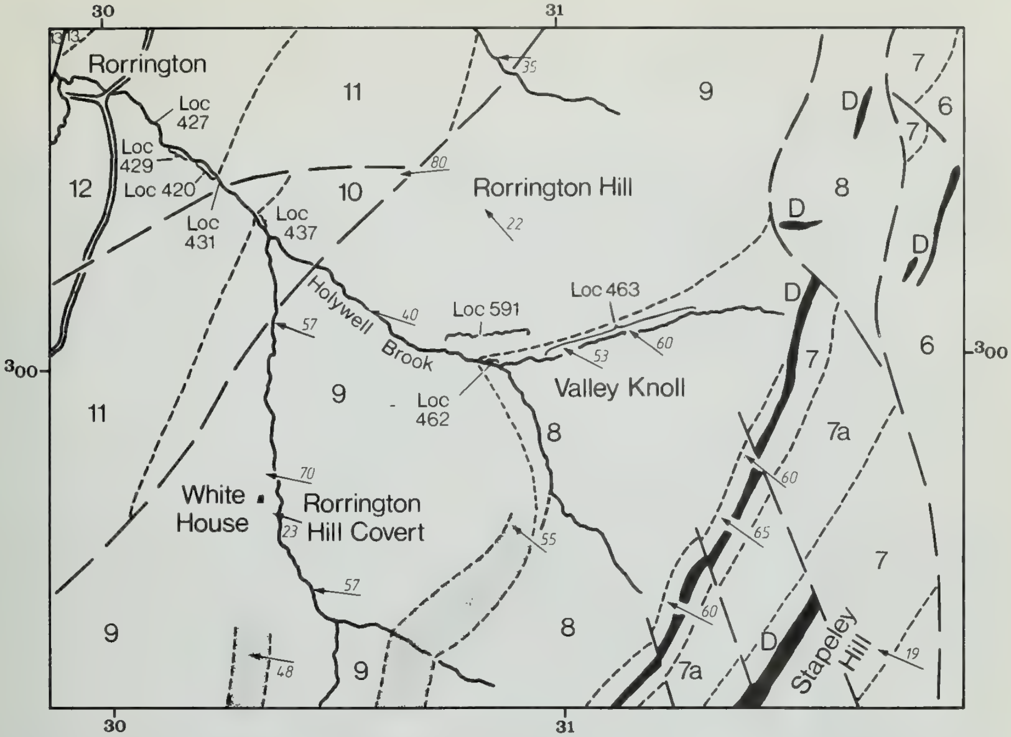
30
31
13
13
Rorrington
Loc 427
Loc 429
12
Loc 420
Loc 431
Loc 437
11
10
35
80
Rorrington Hill
22
9
D
7
6
7
8
D
D
D
Loc 463
Loc 591
40
Holywell Brook
57
53
60
7
6
3oo
3oo
9
Loc 462
Valley Knoll
11
8
7a
60
70
White House
Rorrington Hill Covert
23
55
65
57
7
60
8
9
D
Stapeley Hill
48
9
7a
19
30
31

Fig. 25 Geological map of the area around Holywell Brook, SE of Rorrington. Overlaps Figs 24, 27, 28, 31. 6 = Hope Member; 7 = Stapeley Volcanic Member (7a = interbedded shales); 8 = Stapeley Shale Member; 9 = Weston Member, including 'grit' horizons (dotted); 10 = Betton Member; 11 = Meadowtown Member; 12 = Rorrington Member; 13 = Spy Wood Member; black outcrop D = dolerite. (SO 39, SJ 30)

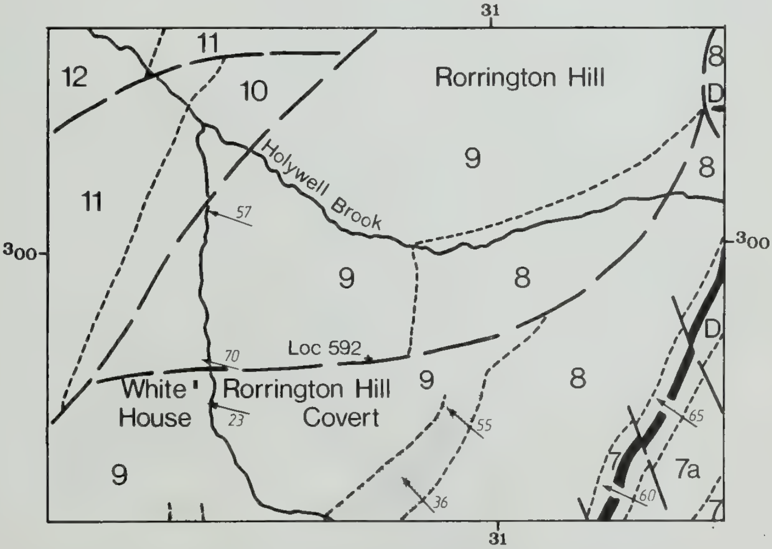
31
11
12
10
Rorrington Hill
8
D
Holywell Brook
9
8
11
57
3oo
3oo
9
8
D
Loc 592
70
White House
Rorrington Hill Covert
9
8
23
55
65
7
7a
9
36
60
7
31

Fig. 26 Alternative interpretation of the area around Holywell Brook; beds as in Fig. 25. Heavy mineralization of rocks at Loc. 592 suggests the proximity of a fault. (SO 39, SJ 30)

SSW of Venusbank (Fig. 15, p. 25). The shales there are underlain by folded and faulted tuffs of the Stapeley Volcanic Member and overlain by unconformable strata of Llandovery age.

Middleton Formation

First usage. As Middleton or Llandeilo Series, by Lapworth & Watts (1910 : 752, 753), underlain by Shelve Series and overlain by Chirbury Series. Made up of successive subdivisions of Weston Flags and Shales (or Stage), Betton or *Didymograptus murchisoni* Shales, Meadowtown Calcareous Beds (or Stage) and Rorrington Shales, the term replaced without comment the earlier-named Meadowtown Series of Lapworth (1887 : 662).

Type locality. Presumably the vicinity of the hamlet of Middleton, 2½ miles (4 km) due west of Shelve, but no type section was designated.

Weston Member

First usage. As Weston Group, by Lapworth (1887 : 662), apparently in the same sense as now employed.

Type locality. 'Priestweston hamlet' was designated by Whittard (1960 : 281) in the *Lexique Stratigraphique International*, where he described the constituent rocks as being 'divided into a lower and upper group of massive greenish-brown grits, separated by rusty-weathering, blue-hearted shales'. This description almost exactly matched one given earlier by him (1931 : 330) except that the 'shales' were listed as 'flags'. In his notes Whittard referred to the old quarry at Priestweston as being the type locality, but with reservations that are discussed later.

Descriptive notes. The rock types within the Weston Member include siltstone, flagstone and tuff, while shale is only rarely developed. One of the characteristics of the more argillaceous strata is that they seldom present a surface sufficiently flat for measuring the dip. The almost total absence of soft shales is a useful factor in distinguishing the rocks from those of the Stapeley Shale Member and the smoothness of the flat, fresh surfaces of the latter beds finds no parallel in the Weston Member. Consequently, even though the boundary of the two members is arbitrarily taken, and there is a gradation through *c.* 20–30 ft (6–9 m) of rock, it is fairly easy to distinguish those belonging to the Weston Member. The strata appear to represent ill-sorted, extremely shallow water deposits which might even be near estuarine in origin. In places they were apparently laid down under turbulent conditions, as shown by the remarkably rapid and irregular alternations of wisps of argillaceous matter within siltstones. Furthermore, the rocks are not generally fossiliferous, but in places they are richly so. Some fossil localities are in the more shaly beds, others are less richly fossiliferous in thin flagstones, others include the occasional occurrences in massive beds, and yet others are associated with tuffaceous layers in which graptolites are not infrequent. The latter may be taken to indicate other than near-estuarine conditions, but it was not unusual for graptolites to enter shallow coastal waters and if they were epiplanktonic no doubt detached masses were sometimes washed into littoral zones. What is more significant is that whenever the beds are found to be fossiliferous, by far the most important elements in the fauna are the bivalves, horny brachiopods and, less commonly, gastropods. Other forms are trilobites, mainly *Ogyginus corndensis* (Murchison), a few nautiloid cephalopods, rare crinoids and some articulate brachiopods. This fauna is not one typical of the shallow waters of the Ordovician sea, and its association with ill-sorted sediments suggests estuarine conditions.

Within the whole outcrop of the Weston Member there are subsidiary escarpments, sometimes pronounced. These scarps are not so much owing to the alternation of soft rocks with much harder ones as to variation in the proportions of grits, flags and shales developed in an interbedded series. Even in the less resistant divisions, alternation of rock-types persists. In some cases the main resistant horizons can be mapped for a moderate distance across country, but in others a single horizon may quickly be replaced by more than one. It is evident that the Weston Member, on both the large and the small scale, is composed of constantly-changing, lenticular strata, a view not inconsistent with deposition in a very shallow water environment.

Outcrops of the Weston Member are confined to the western limb of the Shelve Anticline, where they occupy a strip of country up to about half a mile (0·8 km) wide which extends NNE from a point three-quarters of a mile (1·2 km) ESE of Church Stoke, by way of Priestweston, to terminate at the northern boundary of the Inlier between Betton and Leigh Hall (Map). The most southerly section occurs in an old quarry (Loc. 406), situated near Hoarstone Farm and 4350 ft (1326 m) at 114° true from St Nicholas's church, Church Stoke. In this area the rocks are flaggy, with a high percentage of coarse-grained volcanic dust, and in places there are thin beds of flinty, vitric tuffs and occasional intercalations of soft, friable tuffaceous material. The outcrop narrows northwards between the andesitic mass of Todleth Hill, to the east, and the Quaternary deposits of the Church Stoke area, but widens to the north of Old Church Stoke and underlies the flat ground south and east of Upper Aldress (Map).

A little farther north is Cwm-Dwla (sometimes Cwmdulla) farm, just west of the SW end of Lan Fawr hill (Fig. 23, p. 34), which is of importance as it provides one of only two places (the other is Holywell Brook – see p. 35) where the passage from Stapeley Shale Member to Weston Member can be studied. The section (Loc. 952), situated just behind and north of the farm, shows the Shale Member comprising light-grey weathering, silky shales, dark grey when fresh and interbedded with flags and tuffs which vary in thickness from less than an inch (25 mm) up to 10 in (250 mm). These harder beds appear to increase in importance higher in the succession and eventually give place to the typical Weston Member lithology, with its appearance of argillaceous matter whisked up with silty material.There is no indication of a sedimentary break and, as at Holywell Brook, the succession is undoubtedly continuous. The area immediately north and east of Cwm-Dwla is interpreted as part of a fault-bounded, angular outcrop which includes also Stapeley Shale Member and is truncated to both north and south by transverse faults, the northerly of which coincides with a dolerite intrusion elongated east–west.

Farther north again lies the hamlet of Priestweston, said to be the type locality for the Weston Group and consequently presumed to be that for the Weston Beds (now Weston Member), although in practice only a fraction of the succession is found there. Whittard noted that the old quarry (Loc. 766) at Priestweston might be taken as the type-section but observed that in a sense this would be misleading since it exposes no more than 90 ft (27·5 m) of rock and is excavated in the hardest, flaggy beds, most suitable for local building. There is no indication of the less resistant beds which go to make up so much of the succession elsewhere and which are not infrequently fossiliferous, whereas the massive beds seldom provide fossil remains and probably accumulated under conditions inimical to animals. For the most part the rocks are flaggy, highly micaceous, sometimes ripple-marked, and interleaved with thin siltstones. On the eastern, dip face the surface is literally covered with fucoid markings where the rock face is markedly micaceous. The fucoids are compressed, unbranched, rod-like structures; they show no particular alignment but may cross one another.

The rocks at Priestweston Quarry were mapped by Whittard as part of the upper of two 'grit' horizons which occur in approximately the lower half of the Member and can be traced NNE for almost 2 miles (3·2 km) before apparently dying out in the vicinity of Rorrington Hill Covert, near Holywell Brook (Fig. 25). The 'grit' of Priestweston Quarry crops out *c.* 1700 ft (518 m) NE of the hamlet, in the sides (Loc. 764) of the subsidiary road running NE from the Methodist chapel, and thence to and just beyond the small valley of Cwm Dingle. Farther NE the outcrop is cut by small, transverse faults; it and the overlying strata are intruded by two east–west dolerite dykes about 1800 ft (549 m) WSW of Middleton Hill. The lower 'grit' horizon crops out just SE of Priestweston, in the vicinity of what was once the Miners Arms inn, and continues parallel to the outcrop of the higher 'grit', though extending a little farther (Map), and forms a feature to the SE of Rorrington Hill Covert. The argillaceous strata between the two 'grit' horizons, though infrequently exposed, were seen in a pathside exposure (Loc. 769) 1850 ft (564 m) at 046° true from Priestweston Quarry (Fig. 23, p. 34).

Between Rorrington Hill Covert and Rorrington Hill runs the valley of Holywell Brook, to the north of which (Fig. 25) is a low, cliff-like outcrop (Loc. 591) formed by rocks in the lower part of the Weston Member. The section is so variable that detailed measurements are not practicable, but *c.* 40 ft (12·2 m) of rock are exposed in the cliff, composed of coarse, tuffaceous

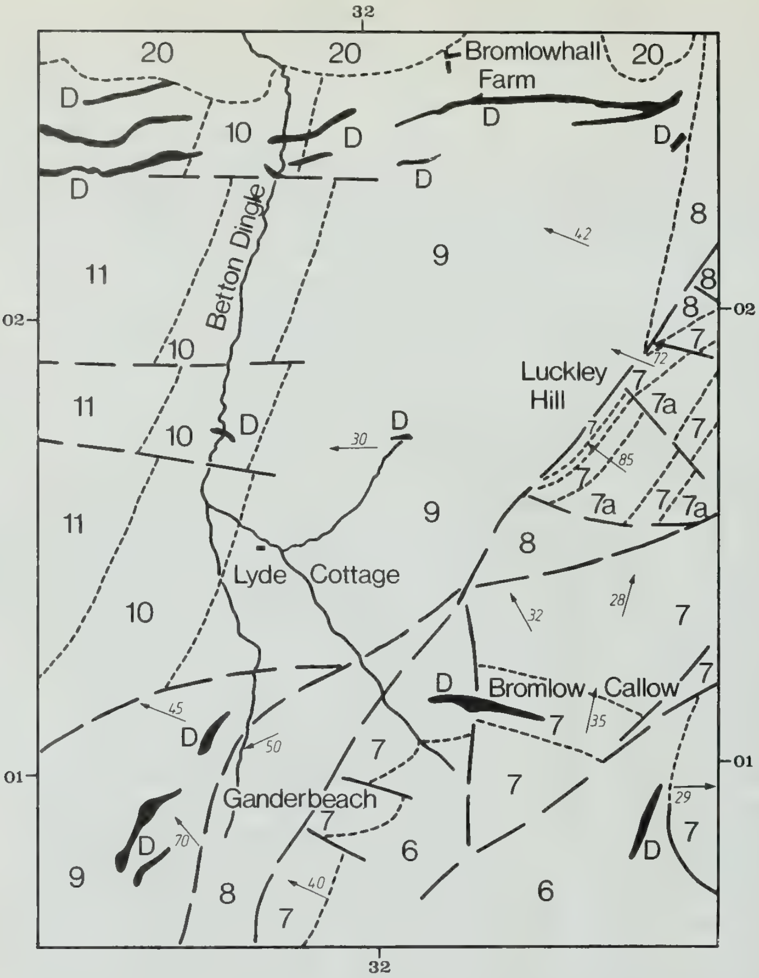
32
20
20
Bromlowhall Farm
20
D
10
D
D
D
D
D
8
42
Betton Dingle
9
11
8
02
02
8
10
7
72
Luckley Hill
11
7
7a
10
D
D
30
7
7
85
11
9
7
7a
7
7a
8
Lyde Cottage
10
28
32
7
D
Bromlow Callow
7
45
7
35
D
50
7
01
01
7
29
Ganderbeach
7
6
D
70
D
7
9
8
40
6
7
32

Fig. 27 Geological map of the area around Betton Hill and Luckley Hill, east of Meadowtown. Adjoins Fig. 28; overlaps Figs 16, 17, 25. 6 = Hope Member; 7 = Stapeley Volcanic Member (7a = interbedded shales); 8 = Stapeley Shale Member; 9 = Weston Member; 10 = Betton Member; 11 = Meadowtown Member; 20 = Silurian rocks; black outcrop D = dolerite. (SJ 30)

flags, finer tuffaceous flags showing curvilinear banding, and knobbly-weathering silty shales. It would seem that the massive beds of the Weston Member owe their massiveness to included volcanic débris, without which the rocks would probably have been deposited as muds and silts. Immediately west of the cliff, an old quarry adds *c.* 40 ft (12·2 m) to the thickness exposed there and is stratigraphically beneath it. The quarry face is mainly built up of fine-grained massive rocks in which small lenses of apparently more tuffaceous material weather more readily.

From Rorrington Hill the outcrop of the Weston Member narrows northeastwards as the result of faulting in the area east of Meadowtown, and then widens again between Lyde and Bromlow (Fig. 27) before being terminated by unconformable Lower Silurian strata between Betton and Leigh Hall. The passage from Weston Member to Betton Member in the stream section near Lyde Cottage (Fig. 27) is assumed to be normal and gradational though the actual junction seems somewhat arbitrary. The angle formed by this stream and a subsidiary one at a point 150 ft (45·7 m) SSE of Lyde Cottage exposes a section in brown-weathering, nodular strata of the Weston Member. This exposure was particularly noted by Whittard (1958 : 13) as showing shales which elsewhere are interbedded with massive flags and which here are unusually fossiliferous.

Betton Member

FIRST USAGE. As Betton or *Didymograptus Murchisoni* Shales by Lapworth & Watts (1910 : 752, 753). The rocks were said to yield an abundance of *D. murchisoni* and *Orthis*, and to be best exposed SE of Rorrington. They were later termed *Didymograptus murchisoni* Beds, equivalent to a Betton Group or Stage, by both Lapworth (1916 : 36) and Watts (1925 : 340), but the name Betton Beds was introduced by Whittard (1931 : 323) and retained by him thereafter.

TYPE SECTION. Betton Dingle, NNE of Meadowtown (Fig. 27), according to Whittard (1960 : 52).

DESCRIPTIVE NOTES. The beds were described by Whittard (1931 : 331; 1960 : 52) as micaceous, blue-black shales and flags with a thickness of 600 ft (183 m), a figure notably larger than the 200 ft (61 m) give earlier by Watts (1925 : 340). Junctions with the underlying Weston Member and overlying Meadowtown Member were said to be apparently gradational.

Lapworth & Watts' geological map of the Shelve Inlier (*in* Pocock & Whitehead 1948 : pl. 11) indicated the outcrop of the 'Betton Shales and Flags' as forming a narrow, unbroken, band-like outcrop which extended SSW from the vicinity of Betton farm to reach the southern boundary about three-quarters of a mile (1·2 km) SE of Church Stoke. Whittard's mapping demonstrated that the outcrop is, in fact, broken into three discrete portions as a result of the north–south tear-faults which affect the Inlier.

The northernmost outcrops of Betton Member occur (Fig. 27) in the vicinity of Betton Dingle, which runs NNE almost along the strike in the area SSE of Betton farm. Only here is the succession complete, with both upper and lower boundaries unaffected by faulting. A conspicuous feature of the outcrops immediately south of the margin of the Inlier, here comprising unconformable Silurian strata, is the presence of narrow, subparallel dolerite intrusions, members of a group which are elongated east–west in the area between Overton's Rough and Lower Wood. The predominantly strike section in Betton Dingle exhibits little variation in lithology. The general rock type is a micaceous, rusty-weathering, blue-hearted shale occasionally interbedded with more siliceous layers which pass into flags, not infrequently colour-banded blue-grey and light grey. At other times volcanic detritus is obviously present, producing coarser-grained rocks.

From here the outcrop continues SSW until level with Meadowtown hamlet, where it is obliquely truncated by a fault so that the outcrop narrows and finally disappears half a mile (0·8 km) east of Rorrington. Exposures of Betton Member are recorded (Fig. 28) from the lane (Loc. 577) 600 ft (183 m) SSE of Meadowtown Quarry, where pendent didymograptids were found, as well as in the fields SW of this point. Loc. 505, 1300 ft (396 m) SW in the stream skirting the north side of Rorrington Hill, shows an exposure in blue-black shales which yielded ogyginid and trinucleid trilobites. Whittard noted that the section here (assuming a uniform dip) contains a thickness of 440 ft (134 m) of Betton Member, a figure comparable with that in Holywell Brook; this is considerably less than the 600 ft (183 m) given elsewhere by Whittard for the Member, but the succession here is incomplete owing to faulting.

The southern continuation of this outcrop is 'stepped' westwards by a fault and the rocks are seen next in the small valleys cut by Holywell Brook and Whitehouse Brook, the stream running north along the western margin of Rorrington Hill Covert (Fig. 25, p. 37). Immediately north of (i.e. downstream from) the junction of the two is a section (Loc. 437) in shales, flaggy and tuffaceous shales, and thin, 1–3 in (2·5–7·5 cm) tuffs, the last containing angular fragments and abundant pyrite. The rocks yielded a varied fauna comprising *Didymograptus* of *murchisoni* type and trilobites (*Ogyginus*, *Bettonia* and *Trinucleus*). The apparent thickness of 400 ft (122 m) is again low because of faulting, as a result of which the next set of outcrops is found farther SW, underlying a wedge-shaped area to the west and, especially, north of Priestweston (Map). The area is not well exposed but at Loc. 307 (Fig. 29), in the stream-section 990 ft (302 m) WSW of Little Weston, may be seen blue-hearted flaggy beds with some very thin, shaly partings; these contain a fauna similar to but less abundant than that at Loc. 437.

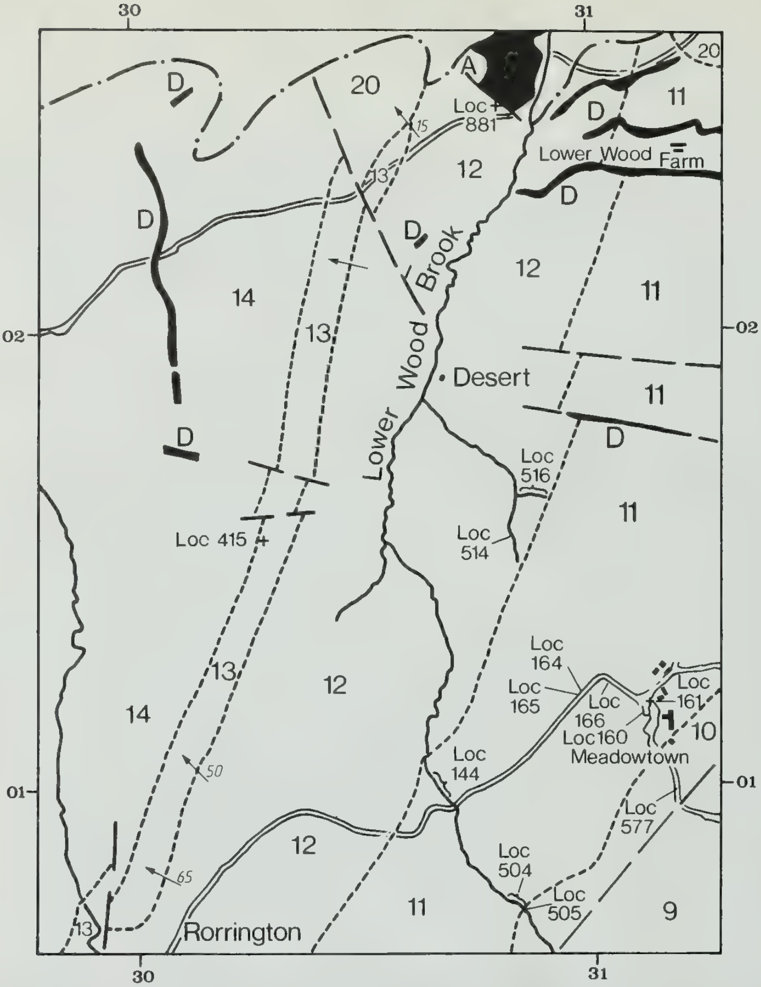
30
31
02
01
20
A
D
11
Loc 881
15
12
Lower Wood Farm
13
Brook
Lower Wood
14
• Desert
Loc 516
Loc 514
Loc 415
Loc 164
Loc 165
Loc 166
Loc 160
Loc 161
10
Meadowtown
Loc 144
50
65
Loc 577
Loc 504
Loc 505
9
Rorrington

Fig. 28 Geological map of the area NW of Meadowtown, including Lower Wood Brook. Adjoins Fig. 27; overlaps Fig. 25. 9 = Weston Member; 10 = Betton Member; 11 = Meadowtown Member; 12 = Rorrington Member; 13 = Spy Wood Member; 14 = Aldress Member; 20 = Silurian rocks; black outcrop D = dolerite; black outcrop A = andestic intrusion of Lower Wood (SJ 30)

The sole remaining outcrops of Betton Member occur in two small, immediately adjacent and largely fault-bounded areas centred about half a mile (0·8 km) north of Church Stoke, where the southerly continuation is terminated by glacial deposits forming the southern boundary of the Inlier. The original interpretation of this area was subject to some later revision by Whittard, and the present map represents his final version.

The uppermost (i.e. easterly) reaches of Spy Wood Brook expose sandy, argillaceous, flaggy beds with much volcanic dust and pyrite at Loc. 382 (Fig. 30). Fossils are not common but include *Ogyginus*, trinucleids, fragments of inarticulate brachiopods and poorly-preserved biserial graptolites. About 750 ft (231 m) farther south, the last outcrops of Betton Member are seen in the small valley known locally and in Whittard's Monograph and notes as Deadman's Dingle, which runs westwards into Spy Wood Brook. Several exposures, including Loc. 385, of micaceous, flaggy shales occur, some of which contain a typical fauna of graptolites and trilobites, while Loc. 384, in the lower part of the succession, shows *c.* 18 ft (5·5 m) of rusty-weathering shales rich in volcanic detritus.

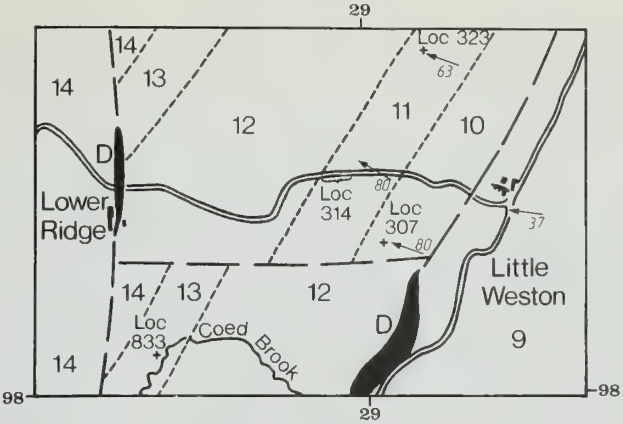

Fig. 29 Geological map of the area between Lower Ridge and Little Weston, including the upper reaches of Coed Brook. Adjoins Figs 23, 34; overlaps Fig. 24. 9 = Weston Member; 10 = Betton Member; 11 = Meadowtown Member; 12 = Rorrington Member; 13 = Spy Wood Member; 14 = Aldress Member; black outcrop D = dolerite. (SO 29)

Meadowtown Member

FIRST USAGE. As Meadowtown Calcareous Beds or Meadowtown Stage, by Lapworth & Watts (1910 : 752, 753). Equivalent to the Meadowtown Group of Lapworth (1916 : 36), later renamed Meadowtown Beds by Whittard (1931 : 323). Further subdivisions of the Meadowtown Group listed by Lapworth (1916 : 36) have not survived. The term should not be confused with 'Meadowtown Series' as used by Lapworth (1887 : 662), a much larger subdivision which is equivalent to the present Middleton Formation.

TYPE LOCALITY. 'Meadowtown hamlet' according to Whittard (1960 : 183), no specific type section being designated.

DESCRIPTIVE NOTES. The rocks were described briefly by Whittard (1931 : 331; 1960 : 183) as comprising blue-black shales and flags with some developments of limestones, calcareous flags and bedded tuffs. A thickness of *c.* 1300 ft (396 m) was given and the contact with the underlying Betton Member described as gradational. Whittard's later lists (1966 : 299–307) of trilobites from the Shelve Inlier showed the trinucleids *Whittardaspis* [*Cryptolithus*] *inopinata* (Whittard) and *Lloydolithus lloydii* (Murchison), and the ogyginid *Ogygiocarella debuchii* (Brongniart), to be especially abundant and characteristic.

The boundaries of the Member as mapped by Whittard at various periods demonstrate changes of opinion but his final word on the subject (1966 : 298) defined the lithostratigraphic boundary with the overlying Rorrington Member as occurring at the point where 'bluish-grey shales with occasional thin, bluish limestones and sometimes bedded tuffs' (in which shelly faunas are abundant and graptolites rare except in a few thin bands) pass upwards into 'massive sooty-black graptolitic mudstones and shales', described as monotonously uniform. The change in fauna was said to be 'much more obvious than the lithological one', but there can be little doubt that one is dealing with a true lithostratigraphic boundary. The thickness of the Meadowtown Member as so interpreted was described by him as being much greater than he originally thought (i.e. in the early parts of the same monograph), and this was reflected also in the modified version of his field slips, on which the outcrop is considerably wider.

Although Meadowtown hamlet was given as type locality it is sited within the outcrop of the lowest third of the Meadowtown Member and for practical purposes the section there is confined to the vicinity of the classic but long-disused quarry, knowledge of which dates from the time of Murchison. The section in Meadowtown Quarry (Loc. 160) was measured by Whittard when it

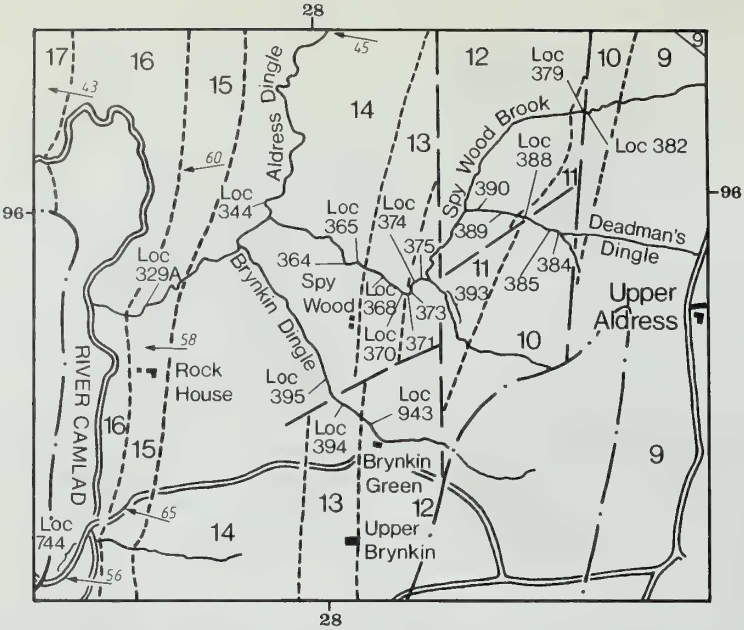
28
17
16
15
14
13
12
Loc 379
10
9
9
43
45
60
Aldress Dingle
Spy Wood Brook
Loc 388
Loc 382
Loc 344
Loc 365
Loc 374
390
389
375
96
96
Deadman's Dingle
Loc 329A
364
Spy Wood
Brynkin Dingle
Loc 368
373
11
11
393
385
384
Upper Aldress
58
Loc 370
371
10
Rock House
Loc 395
Loc 943
RIVER CAMLAD
16
15
Loc 394
Brynkin Green
9
65
13
12
Loc 744
14
Upper Brynkin
56
28

Fig. 30 Geological map of the faulted area around Spy Wood, NNE of Church Stoke. Overlaps Figs 23, 32. 9 = Weston Member; 10 = Betton Member; 11 = Meadowtown Member; 12 = Rorrington Member; 13 = Spy Wood Member; 14 = Aldress Member; 15 = Hagley Volcanic Member; 16 = Hagley Shale Member; 17 = Whittery Volcanic Member. (SO 29)

was reopened in 1932 and listed by him (1952 : 160). He noted that the *c*. 32 ft (9·75 m) of rock exposed could be divided into three parts:

3. Shales, 12 ft (3·66 m),
2. Mainly limestone, nearly 10 ft (3 m),
1. Flags, shales and limestones, nearly 10 ft (3 m).

To the east of the quarry and in the nearby roadway (Loc. 161) an underlying succession of flaggy, calcareous beds with bands of ashy material added a further 66 ft (20 m) of strata. West of the quarry and along the road leading towards Rorrington (Locs 164–6) successively higher levels were mapped. Near the point where the same road crosses Lower Wood Brook, a tributary of Desert Brook (Fig. 28, p. 42), and immediately NW along the stream, are exposures of blue-black mudstones (Loc. 144) with layers up to 3 in (76 mm) thick of small, black, nodular concretions about the size of a pea. These strata were originally mapped by Whittard as Rorrington Member but were later reinterpreted as Meadowtown Member. SE of the same road/stream junction, exposures throughout much of the Member are marked sporadically along Lower Wood Brook; the apparently lowest beds visible are marked at Loc. 504, where they comprise hard mudstones with massive bands of fine-grained tuffaceous material, and the lower boundary of the Member is drawn between this point and the nearby Loc. 505 which exposes blue-black, micaceous shales of the Betton Member.

The outcrop of the Meadowtown Member extends NNE from the eponymous hamlet as a broad strip that is 'stepped' westwards slightly at each of three small east–west faults, two of which coincide with dolerite intrusions, and ends beneath uncomformable Lower Silurian strata a short distance north of Betton Wood farm (Map). The northern half of this area is not well exposed but several outcrops are recorded in the vicinity of Mincop, and between there and Meadowtown.

SW of Meadowtown and beyond Lower Wood Brook, the Meadowtown Member extends SW to Holywell Brook at a point *c*. 1000 ft (305 m) SE of Rorrington, where the outcrop is shifted westwards on the south side of an arcuate, approximately ENE–WSW fault. The brook section SE of Rorrington (Fig. 25, p. 37) is of interest because, as a result of the faulting, one finds within the comparatively short distance of *c.* 450 ft (137 m) both Meadowtown/Rorrington and Betton/Meadowtown boundaries. The latter was not actually observed at the point where the mapped line is drawn (south of the arcuate fault), but the highest part of the Betton Member comprises the rocks at Loc. 437, described on p. 41. North of the fault, Loc. 431 marks the highest Meadowtown Member, and the adjacent section of Loc. 420 is assigned to the lowest part of the Rorrington Member.

The outcrop of the Member continues to the SW (Fig. 24, p. 36), so that shales and flags are exposed in the lane section (Loc. 470) near and SE of Middleton vicarage, to the south of which it narrows between two converging faults. The westerly of these is one of the large north–south tear faults which cut the Inlier, and to the west of it the outcrop of the Meadowtown Member appears narrower as the dips are steeper. At the top of the wooded area *c.* 1200 ft (366 m) NNW of Little Weston (Loc. 323) are small outcrops of usually tuffaceous shales and sandy, flaggy beds together with interbedded tuffs, some containing nodules, possibly calcareous (Fig. 29, p. 43). A short distance along the strike is the lane leading west from Little Weston, where Loc. 314 showed bluish-black shales with interbedded, thin, up to 3 in (76 mm) bands of limestone, decalcified marginally; the beds are almost vertical, but there is some hill creep. The outcrops of this area are truncated to the south by an east–west fault, to the south of which Meadowtown Member was shown in Whittard's original mapping, an interpretation subsequently modified to show a large outcrop of Rorrington Member underlying the feature of Spy Wood Member running along part of the upper reaches of Coed Brook (see p. 43).

Beyond the fault only two other outcrops of Meadowtown Member are encountered. The first, centred on the stream section about quarter of a mile (0·4 km) SW of Priestweston, is sub-rhombic in outline, divided into two unequal parts by the north–south tear fault noted above. In the eastern part, flags and sandy shales at Loc. 354 (Fig. 23, p. 34) yielded fragmentary fossils including *Ogygiocarella debuchii* and *Whittardaspis* sp. The western part is less well exposed but a small outcrop (Loc. 944) in a ditch, not noted in the earlier mapping, contained *O. debuchii* and *Lloydolithus lloydii.*

About half a mile (0·8 km) SSW and located between the same north–south tear fault and a subparallel fault sited a short distance to the west, is a small outcrop of Meadowtown Member centred *c.* 1500 ft (457 m) NW of Upper Aldress (Fig. 30, p. 44). The two halves of the outcrop are separated by one of the complementary shear faults associated with the tear faults. The northern half extends as a narrow strip between the stream sections of Deadman's Dingle (see description of Betton Member, p. 42) and the upper reaches of Spy Wood Brook. In the former section, Loc. 388 exposed dark, micaceous, blocky shales with numerous *O. debuchii*, rare *Primaspis* and inarticulate brachiopods; the rocks are faulted against those of the Betton Member, which may be seen a short distance upstream. The latter section (Loc. 379) exposes blue, fine-grained limestones and sandy shales with interbedded ashy bands which contain abundant pyrite and volcanic material mixed with argillaceous material; shale pellets and irregular, phosphatic nodular masses also occur. The southern half of the outcrop, triangular in outline, is cut by a small tributary stream which runs NW to Spy Wood Brook. The section (Loc. 393) shows rocks of the Rorrington Member at its NW end, cut by calcite veins and separated by a fault from dark-grey limestones and greenish-grey shales, both of which contain volcanic material, assigned to the Meadowtown Member. A few fossils are reported, including *O. debuchii*, inarticulate brachiopods and *Dicellograptus.* Immediately SE of the stream section, the Ordovician outcrops are terminated by glacial deposits forming the southern boundary of the Shelve Inlier.

Rorrington Member

First usage. As Rorrington Group by Lapworth (1887 : 662), a term subsequently modified to Rorrington Flags (Lapworth & Watts 1894 : 316, 318) and Rorrington Shales (Lapworth & Watts 1910 : 752) but with no apparent difference in meaning. A change to Rorrington Group or Stage, subdivided into successive Nemagraptus Beds and Leptograptus Beds (Lapworth 1916:

361; Watts 1925: 340) was abandoned by Whittard who (1931: 323, 332 and subsequent papers) preferred the term Rorrington Beds, corresponding to the present Member.

TYPE LOCALITY. Lower Wood Brook, near Rorrington (Whittard 1960 : 237).

DESCRIPTIVE NOTES. The rocks were described as sooty, blue-black shales *c.* 1000 ft (305 m) thick by Whittard (1931 : 332; 1960 : 237) who assigned them to the *Nemagraptus gracilis* Zone and listed numerous species of graptolites and trilobites. As pointed out elsewhere (Dean *in* Williams *et al.* 1972 : 41), further refinement of the correlation between both Meadowtown and Rorrington Members and the corresponding graptolite zones must await description of the appropriate faunas.

In general, the outcrop of the Rorrington Member forms a broad band running SSW across the Inlier parallel to that of the Meadowtown Member. In an earlier version of Whittard's map the Rorrington outcrop was almost three times as broad as that of the Meadowtown Member, but following his later revision of the boundary between the two the outcrops were shown as of subequal breadth. The northernmost extension of the outcrop meets the superficial deposits forming the northern boundary of the Inlier in the vicinity of Lower Wood farm, where the beds are intruded by both dolerite dykes and a mass of dolerite (Map), and to a small extent are unconformably overlain by Lower Silurian strata. At the SW end of the quarry near Lower Wood farm the igneous rock, which was worked to a depth of 70 ft (21·3 m), is thrust over shales of the Rorrington Member. One small *Dicellograptus* ? and two minute ogyginid trilobites were found in the shales, of which a section (Fig. 28, p. 42) of 24 ft (7·3 m) was seen (Loc. 881), and the beds show no sign of metamorphism other than a hardening which might be due to mineralization along the contact rather than to heat. The igneous rock, which appears to be in the form of a boss, shows no chilled margin and on intrusion caused little induration of the shale.

The valley of Lower Wood Brook runs SSW from the eponymous farm for about three-quarters of a mile (1·2 km) and intermittent exposures of Rorrington Member appear. Unfortunately the stream runs approximately along the strike so that the exposures cover little more than a quarter of the total thickness. However, the valley of an unnamed tributary stream, which runs NW to join Lower Wood Brook a short distance upstream from the building named Desert, provides important information and may be regarded as a supplementary type locality as it shows several exposures in what is almost a dip section through the lower half of the Member (Fig. 28). Beds of the typical lithology were recorded at Loc. 516 though those at the eastern end were said to be a little more thickly bedded. *Ogygiocarella debuchii* was listed from the lowest fossiliferous strata there, and was recorded in association with *Marrolithoides arcuatus* Whittard slightly higher in the sequence. A short distance SSW along the strike, strata apparently at about the same horizon as the highest exposed at Loc. 516 were shown at Loc. 514, but containing a more varied fauna which included *Dicellograptus*, ostracods, inarticulate brachiopods and the trilobites *Primaspis whitei* Whittard and *Spirantyx calvarina* Whittard in addition to *O. debuchii.*

Slightly more than three-quarters of a mile (1·2 km) SSW, the valley of Holywell Brook also provides a dip section through the Rorrington Member, though it lacks exposures in the middle portion such as are found in Lower Wood Brook. On the other hand, it does show the lowest strata and, supplemented by the section in its tributary stream Grey Grass Dingle (Fig. 31), much of the highest part of the succession, though the boundary with the Spy Wood Member is obscured by a small fault. As noted earlier, Loc. 431 in Holywell Brook (Fig. 25, p. 37) exposes highest Meadowtown Member, with *O. debuchii*, *Cnemidopyge granulata* Whittard and ostracods. The closely-adjacent Loc. 420 shows shales with sandy shales or siltstones, and higher beds become progressively less resistant to weathering. Only inarticulate brachiopods were recorded there but the succeeding strata at Loc. 429 yielded *O. debuchii*, *C. granulata*, *S. calvarina* and *M. arcuatus*, while the rocks were said to include thin, up to 9 in (22·9 cm) bands of fine-grained tuffs in addition to shales of the usual type. The stream section continues as far as Loc. 427, but succeeding strata were seen only at Grey Grass Dingle, a short distance SW. Whittard's notes draw attention to the fact that these higher beds are poorly fossiliferous and speculate that the same may be true of all the higher beds of the Rorrington Member. Although fossils are so scarce

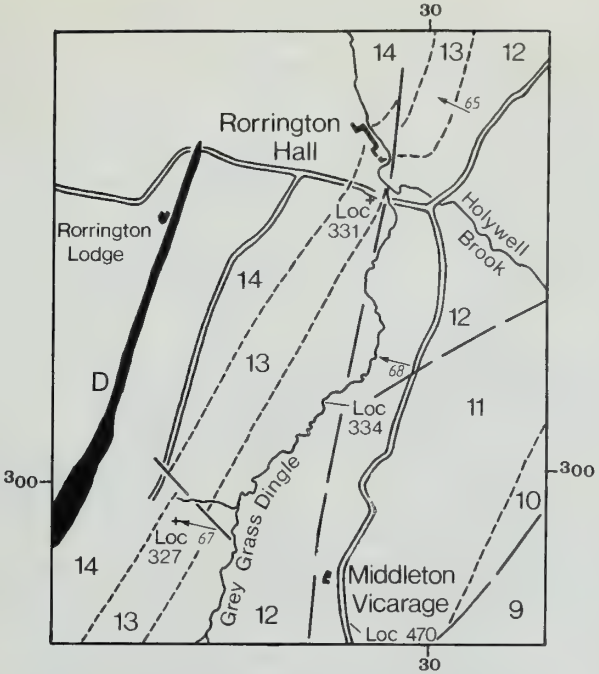

Fig. 31 Geological map of the area SW of Rorrington. Overlaps Figs 25, 28. 9 = Weston Member; 10 = Betton Member; 11 = Meadowtown Member; 12 = Rorrington Member; 13 = Spy Wood Member; 14 = Aldress Member; black outcrop D = dolerite. (SO 29, SO 39, SJ 20, SJ 30)

at Grey Grass Dingle, Loc. 334 is of interest as having yielded *Nemagraptus* in addition to *O. debuchii* and *M. arcuatus*.

The remaining outcrops of the Rorrington Member occupy a not inconsiderable area but, owing to the regressively-weathering nature of the rocks, reveal few exposures. In the area west of Little Weston, at and around the head-waters of Coed Brook, no exposures are documented on Whittard's maps and the outcrop is apparently delimited on the basis of the Spy Wood and Meadowtown Members, both of which are more clearly recognizable.

South of the ENE–WSW fault already noted near Little Weston, p. 45, the outcrop is shifted eastwards and its eastern boundary is faulted against the Weston Member of the Priestweston area. The mapped outcrop of the Rorrington Member is fairly extensive but, again, sections are few though a small tributary stream of Coed Brook shows exposures of rocks in the highest part of the Member *c.* 1850 ft (564 m) at 101° true from Hagley farm. From west to east there are good exposures at first of fine-grained, medium-grey, tuffaceous grit, followed by blue-hearted, rusty-weathering shale. Then, at Loc. 309, there are more massive beds traversed by numerous calcite veins. The shaly partings at this locality yielded *Marrolithus bilinearis* Whittard, a species generally found in the Spy Wood Member, and a single specimen of *Platycalymene duplicata* (Murchison) was recorded (Whittard 1960*a* : 156). Farther east in the same section, Loc. 310 exposed fossiliferous, blue-hearted, micaceous shale interbedded with bands of tuff up to 9 in (23 cm) thick; recorded fossils include rare *Spirantyx calvarina* and abundant ostracods, and some of the specimens were said to be preserved in pyrite.

About 1200 ft (366 m) NNE of Lower Aldress (Fig. 32) another east–west tributary of Coed Brook shows several exposures of shales together with some massive flags in the western part of the section, where the beds are faulted against the Aldress Member. Few fossils were found but *Leptograptus* and *Nemagraptus* were recorded at Loc. 351.

The southernmost exposures of this large, elongated outcrop occur in the faulted area of Spy

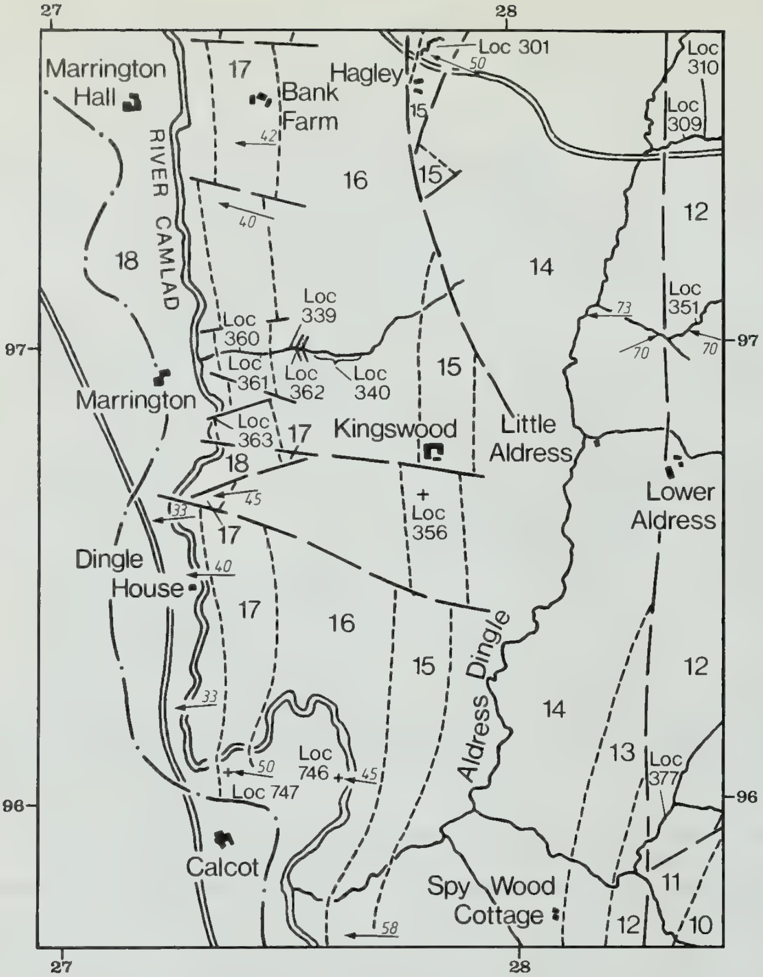
27
28
Loc 301
50
Loc 310
Loc 309
Marrington Hall
17
Bank Farm
Hagley
15
42
16
15
12
40
RIVER CAMLAD
18
14
Loc 339
Loc 360
Loc 361
Loc 362
Loc 340
15
73
Loc 351
70
70
97
Marrington
Loc 363
17
Kingswood
Little Aldress
18
45
33
+ Loc 356
Lower Aldress
17
Dingle House
40
17
16
15
Aldress Dingle
12
14
33
13
Loc 377
Loc 746
50
45
Loc 747
96
Calcot
Spy Wood Cottage
11
12
10
58

Fig. 32 Geological map of the area east of Marrington. Overlaps Figs 23, 30, 33. 10 = Betton Member; 11 = Meadowtown Member; 12 = Rorrington Member; 13 = Spy Wood Member; 14 = Aldress Member; 15 = Hagley Volcanic Member; 16 = Hagley Shale Member; 17 = Whittery Volcanic Member; 18 = Whittery Shale Member. (SO 29)

Wood Brook and part of its small tributary Deadman's Dingle, where a fairly continuous section in the lower half of the Member can be pieced together (Figs 30, p. 44, and 32). In the Spy wood Brook, rusty-weathering shales about the middle of the Rorrington Member occur at Loc. 377, where they yielded *S. calvarina* and *P. whitei*. The locality is just east of the fault separating the rocks from others forming the highest part of the same Member in which several localities, including 373–5, occur only a short distance below the base of the Spy Wood Member and contain a few fossils including *Marrolithoides arcuatus*. Higher upstream, and consequently lower in the succession, are poorly fossiliferous micaceous shales, weathering dark brown, underlain by nodular, greenish-grey siltstones. In Deadman's Dingle, rocks of the Meadowtown Member at Loc. 388 (see p. 45) are succeeded by shales of the Rorrington Member. Loc. 389, only slightly higher in the succession, proved poorly fossiliferous but yielded inarticulate brachiopods and a few graptolites (*Nemagraptus* ? and *Dicellograptus*) and was followed by beds of typical lithology at Loc. 390 containing *O. debuchii* and *S. calvarina*. Strata in the highest part of the Rorrington Member are seen also in Brynkin (= Bryncyn) Dingle, where *O. debuchii* and *S. calvarina* were recorded from shales at Loc. 943. These are the most southerly outcrops of the Rorrington Member, and only a short distance to the south and SE the rocks are overlain by glacial deposits.

Chirbury Formation

First usage. As Chirbury Series (Lapworth 1887 : 662), the highest of three 'Series' of the Shelve Ordovician rocks and underlain by Meadowtown (later Middleton) Series. The term remained in constant use by both Lapworth and Watts until 1925 and was then abandoned without explanation.

Type locality. Presumably the area east of Chirbury village, but no type section was designated.

Spy Wood Member

First usage. As Spy Wood Calcareous Grit, the lower of two subdivisions of the Aldress Group proposed by Lapworth (1887: 662). Later abbreviated to Spy Wood Grit by Lapworth & Watts (1894 : 316), the lower half of a newly-introduced Spy Wood Group (=Aldress Group of 1887).

Type locality. Spy Wood Brook (known alternatively as Spy Wood Dingle, Burn or Bourn), NNE of Church Stoke (Whittard 1960 : 253).

Descriptive notes. Whittard (1931 : 332) described the rocks as flaggy, calcareous sandstones with interbedded greyish shales, weathering olive-green, which assumed a greater importance higher in the succession. The sandstones, when decalcified, were said to contain well-preserved fossils and there was an imperceptible passage upwards into the Aldress Shales (now Aldress Member). In a later paper (Whittard 1960 : 253) the thickness was given as 300 ft (91·4 m) and the strata were said to belong to the *Diplograptus multidens* Zone.

The southernmost extension of the Spy Wood Member is in the vicinity of Upper Brynkin and Brynkin Green (Fig. 30, p. 44), in which area it forms a feature that is covered to the south by glacial deposits forming the margin of the Shelve Inlier. To the north it is 'stepped' NE by two small faults which converge east and bound a small, triangular 'block', exposed (Loc. 394) in the small tributary stream of Coed Brook which runs NW from Brynkin Green and is shown in the manuscript notes, though not on the 6 in to 1 mile (1 : 10 560) O.S. map, as Brynkin Dingle.

More extensive exposures occur at several points in and near the stream which runs through Spy Wood and *c.* 450 ft (137 m) NE of Spy Wood Cottage (Fig. 30). Almost in the centre of the stream section is a good exposure (Loc. 368) of a small anticlinal fold pitching SW at 35°. The rocks in this vicinity are massive, highly micaceous, rusty-weathering flagstones, up to 1 ft (30 cm) thick, interbedded with sandy shales carrying globules of pyrite. Farther east along the same stream, the boundary of the Spy Wood Member and underlying Rorrington Member is exposed in the south bank (Loc. 370). Graptolitic strata of normal Rorrington lithology (Loc. 371) are followed by 9 ft (2·74 m) of micaceous, bluish-grey shale with interbedded thin bands of grey, micaceous, unfossiliferous flagstone. These are succeeded in turn by 12 ft (3·66 m) of more massive beds of typical Spy Wood lithology and it is at the base of these strata that the base of the Member is drawn. The sequence is apparently a normal one with no evidence of a basal conglomerate or angular discordance, and the presence of these unfossiliferous passage-beds at the top of the Rorrington Member was described briefly by Whittard (1952 : 163).

The western end of the same stream section demonstrates the transition between the Spy Wood and overlying Aldress Members. Although no continuous section is exposed the story, again, is one of gradual lithological change, with no evidence of a sharp lithological break at which to draw the boundary. Loc. 365 (Fig. 30) was considered by Whittard to be in the Aldress Member, and the boundary with the underlying Spy Wood Member was drawn at a point 52 ft (15·85 m) upstream (i.e. to the east). On this interpretation the upper beds of the Spy Wood Member comprise flagstones alternating with soft shales and flaggy, sandy shales, all showing various tones of grey and weathering to a dark, rusty colour which is characteristic also of the Aldress Member. The beds are much less massive than those in the lowest part of the Member, and the subdivision may be looked upon as forming the arenaceous base to the Aldress Member.

The Spy Wood Member is mapped as a feature NNE from Spy Wood Brook for *c.* 2000 ft (610 m), when it is truncated by a north–south tear fault running through Lower Aldress farm (Fig. 32, p. 48). It is not seen again until the vicinity of Lower Ridge farm, 1½ miles (2·4 km) east of Chirbury, where it reappears on the east side of the same north–south fault and forms a small, elongated outcrop along part of Coed Brook (Loc. 833 – Fig. 29, p. 43). A short distance north of Lower Ridge, a further subparallel outcrop recommences and continues NE intermittently to Rorrington Hall. There is little of note in this stretch, but the outcrop is 'stepped' by occasional faults of relatively small throw and (Fig. 31, p. 47) at Loc. 327, 2410 ft (735 m) at 045° true from Kinton farm, a mile (1·6 km) SW of Rorrington Hall, yielded two well-preserved brittle-stars in a bed less than 1·57 in (4 cm) thick within a succession that includes mainly sandy, micaceous, brown shales. At Loc. 331, 300 ft (91·4 m) south of Rorrington Hall and just inside the gate on the footpath to Kinton, beds low in the Member are exposed. They comprise micaceous, blue-black shales but, as the succession is ascended, sandy beds and flagstones appear alternating with the shales, some of which are sandy. It was here that an impersistent bed 1½ in (38 mm) thick yielded several starfish. Still higher in this dip section there is a progressive increase in sandstones until one reaches the typical so-called 'Beyrichia grits' of earlier authors, in which ostracods commonly occur in bands but are comparatively rare in the intervening strata. It was from this section that the type material of *Tetradella salopiensis* Harper (1947 : 351) was obtained.

The stream section immediately behind and NE of Rorrington Hall is not straightforward, owing to faulting, but probably represents the approximate thickness of the Spy Wood Member. None of the beds are true shales; all contain some sandy material, the more sandy ones pass into tough siltstones or fine-grained sandstones, and many are quartzitic in appearance. The SE end of the section would appear to indicate an upward passage from the Rorrington Member, with a progressive increase in flaggy beds. It is important to note that the rocks seem virtually unfossiliferous because they are not sufficiently weathered; when weathered, they may be richly fossiliferous in certain bands, and this condition was noted also in other sections, for example Spy Wood Brook.

From Rorrington Hall the outcrop of the Spy Wood Member extends (Fig. 28, p. 42) NNE, broken occasionally by small faults, to terminate at the northern boundary of the inlier about half a mile (0·8 km) west of Betton Wood Farm, where the rocks are overlain unconformably by Upper Llandovery strata which are themselves succeeded by Quaternary and Recent deposits. The beds form a mappable feature and débris rather than exposure tends to be the rule, but one outcrop (Loc. 415), 2900 ft (884 m) at 026° true from Rorrington Hall, is of particular interest as some of the rocks there (not those which are argillaceous or micaceous) yielded fossils which include the zonal trilobite *Costonia ultima* (Bancroft), indicating an age high in the Costonian Stage of the type Caradoc Series.

Aldress Member

First usage. As Aldress Graptolithic (*sic*) Shale, the upper of two subdivisions of the Aldress Group, by Lapworth (1887 : 662). No description was given and the term subsequently came into general use as Aldress Shale or, usually, Shales.

Type locality. Aldress Dingle, 1½ miles (2·4 km) NNE of Church Stoke, west Salop.

Descriptive notes. Brief accounts by Whittard (1931 : 333; 1960 : 32) described the rocks as grey or greenish-brown, soft shales with occasional bands of tuffaceous material in which the fossil assemblage is different from that found in the shales. The thickness was said to be *c.* 1000 ft (305 m), and the beds were assigned to the *Diplograptus multidens* Zone.

In the north of the Shelve Inlier, rocks of the Aldress Member underlie a strip of country, with a maximum width of some 0·7 mile (1·13 km) where affected by faulting but generally much less, which extends to a point half a mile (0·8 km) NE of Wilmington and is bounded to east and west by, respectively, the features of the Spy Wood and Hagley Volcanic Members. Striking physiographic features of this northern area are formed by elongated dolerite intrusions within the shale outcrop between Kinton and Rorrington Lodge, and to the east of Wilmington (Map), but the shales themselves are not well exposed.

The stream section running north almost along the strike from Rorrington towards Wilmington is excavated mainly in glacial deposits, but shows intermittent outcrops of shales and tuffs in the lowest third of the Member. A better section, in the highest strata and noted briefly by Whittard (1931 : 333), is that cut by the stream in Ox Wood (= Ox Wood Dingle), mid-way between Wotherton and Rorrington (Map), where several localities, some graptolitic, are marked on the manuscript map.

No notable sections are shown in the continuation of the overall outcrop SSW to the vicinity of Hagley, though small, scattered outcrops are found, particularly in stream sections. From Hagley southwards, however, there is an increase in the degree of availability of the rocks, particularly along the type section of Aldress Dingle (Fig. 32, p. 48), though the latter suffers from the disadvantage of being excavated almost along the strike and cuts mainly the middle and upper parts of the Member. Loc. 344 (Fig. 30, p. 44), 1750 ft (533 m) at 079° true from Calcot, is of interest as having provided the type material of *Dictyonema fluitans* Bulman (1928 : 35). Two dip sections along streams running east–west in the area immediately north of Lower Aldress farm show the lower beds of the Member, but the boundary with the underlying Spy Wood Member is seen satisfactorily only in Spy Wood Dingle, north of Spy Wood Cottage, noted on p. 49. The rocks in the lowest part of the Member here (Locs 364, 365) are medium-grey in colour but many comprise micaceous siltstones and flags rather than shales, and bedding planes are not always clearly developed (Fig. 30).

A further supplementary section is found in Brynkin Dingle, a term used by Whittard for a tributary of Aldress Dingle (Fig. 30). The lowest beds exposed (Loc. 395) are shales with grey, micaceous flagstones up to a foot (30·5 cm) thick, below which is a thin, inch (2·5 cm) band of white, shaly material, possibly a bentonite and perhaps one of the occurrences noted for the Aldress Member by Whittard (1952 : 164). Shales with flags in the highest part of the Aldress Member were noted in Aldress Dingle only a short distance upstream from the mapped base of the Hagley Volcanic Member, but no detailed account of the boundary was given. From Aldress Dingle to the southern margin of the Inlier, the only outcrops of Aldress Member shown on the manuscript map are some exposures of shale along the stream section which runs westwards to join the Camlad about 500 ft (152 m) NE of Alport. The outcrop was not numbered and no notes were made.

Hagley Volcanic Member

FIRST USAGE. As 'Hagley volcanic ashes and shales' (Lapworth 1887 : 662), a term equivalent to the present Hagley Volcanic Member and Shale Member combined. 'Hagley Ash' was separated by Lapworth & Watts (1894 : 316, 318) and later passed into general use as the Hagley Volcanic Group (Whittard 1931 : 323), equivalent to the present Member.

TYPE LOCALITY. Hagley Quarry, near Chirbury (Whittard 1960 : 145).

DESCRIPTIVE NOTES. In a brief note on the subdivision Whittard (1931 : 333) stated: 'This contains massive crystal and lithic tuffs, which are often brecciated and agglomeratic. The normal rock is of a pale greenish colour, brindled with darker green rings'. Later (Whittard 1952 : 164) he gave a thickness of 350 ft (106·7 m) and noted that at Hagley Quarry graptolitic evidence of the *clingani–linearis* Zones had been found. The latter interpretation has now been superseded and the Member is known to belong to the Lower Soudleyan Stage of the Caradoc Series, equated with part of the *Diplograptus multidens* Zone.

The northernmost limit of outcrop is in the area between Wotherton and Wilmington, where volcanics form a wide feature at Big Cuckoo Nest and Little Cuckoo Nest, just west of Ox Wood Dingle (Map and Fig. 34). The strip-like outcrop here runs SSW through the eastern half of Crest Wood, displaced by small east–west faults, but owing to strike faulting it becomes markedly narrower towards the south end of the wood where it is truncated by a prominent north–south tear fault which displaces the outcrop dextrally. On the west side of this fault the outcrop is shifted NW as far as Rockabank farm and from there to the south forms a feature which extends to Hagley farm (Figs 33–34).

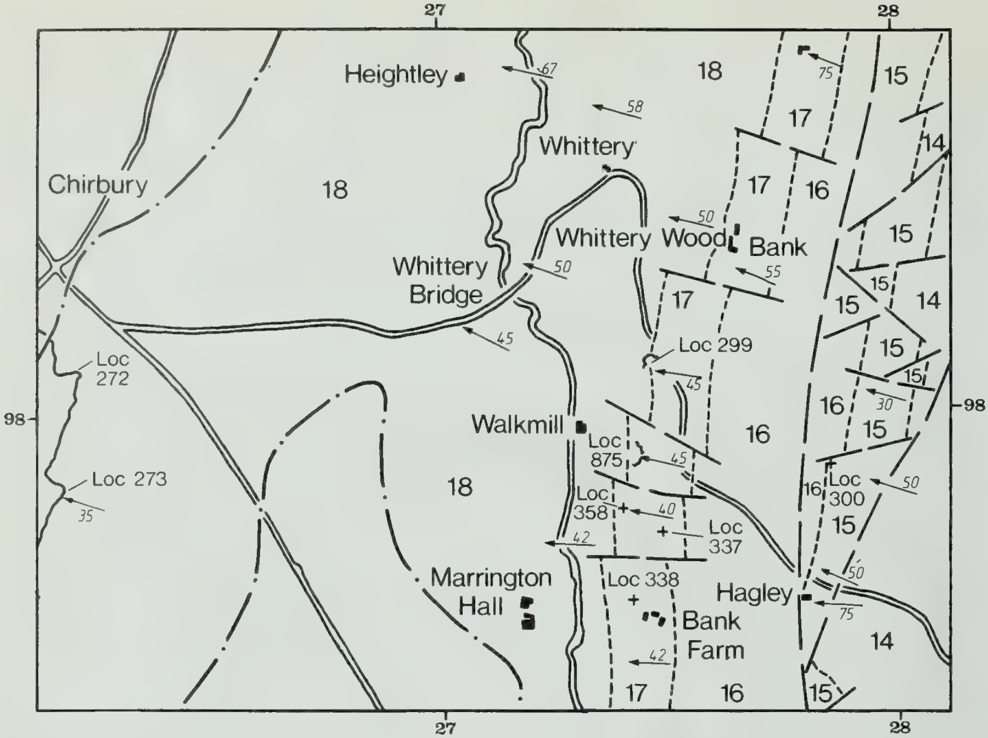

Fig. 33 Geological map of the Whittery area, east of Chirbury. Overlaps Fig. 32. 14=Aldress Member; 15=Hagley Volcanic Member; 16=Hagley Shale Member; 17=Whittery Volcanic Member; 18=Whittery Shale Member. (SO 29)

Hagley Quarry (Loc. 301), the type locality, lies just north of Hagley farm and by the side of the Chirbury–Priestweston road. The area is poorly exposed and although the map shows the upper boundary of the Volcanic Member almost coincident with the western margin of the roadside quarry, the stratigraphical base is not visible here owing to a fault which runs from Upper Ridge farm to Hagley farm and intersects the strike at an acute angle. Hagley Quarry is of particular interest for having yielded graptolites, which were collected from water-deposited tuffs by members of the Geological Survey. The fauna, listed by Whittard (1931 : 333–334), was originally quoted as indicating the topmost *clingani* or basal *linearis* Zone, a widely-quoted but mistaken interpretation that has since been modified to *multidens* Zone (see above). At a point 1000 ft (305 m) just east of north from Hagley farm, and on the western edge of the same volcanic feature, are the remains of an old adit (Fig. 33) from which, according to Whittard's notes, both barytes and (at depth) galena were at one time obtained (Loc. 300).

Apart from a small break just south of Hagley, the feature of volcanic rocks extends southwards to Church Stoke village. Tuffs and agglomerates are seen at Kingswood farm (Fig. 32, p. 48), and an old quarry (Loc. 356) 300 ft (91·5 m) south of the building shows a good exposure in greyish-yellow weathering, lithic tuff with interbedded agglomerate. 'Throstle-breasted' and other types of tuff crop out (Loc. 382A) 3200 ft (975 m) at 190° true from Kingswood (Fig. 32, p. 48), near the ford in Aldress Dingle and a short distance from the River Camlad, but otherwise there is little of note until one reaches the roadside quarry (Loc. 399) 450 ft (137 m) north of Church Stoke Hall. At this point tuffs, interbedded with shales and showing false ripple-marking, yielded the trinucleid trilobites *Broeggerolithus* cf. *broeggeri* (Bancroft) and *Salterolithus caractaci* (Murchison), indicating a Lower Soudleyan age within the Caradoc Series. Intermittent outcrops of tuffs continue south for *c.* 1500 ft (457 m) before disappearing beneath glacial deposits (Fig. 35, p. 55).

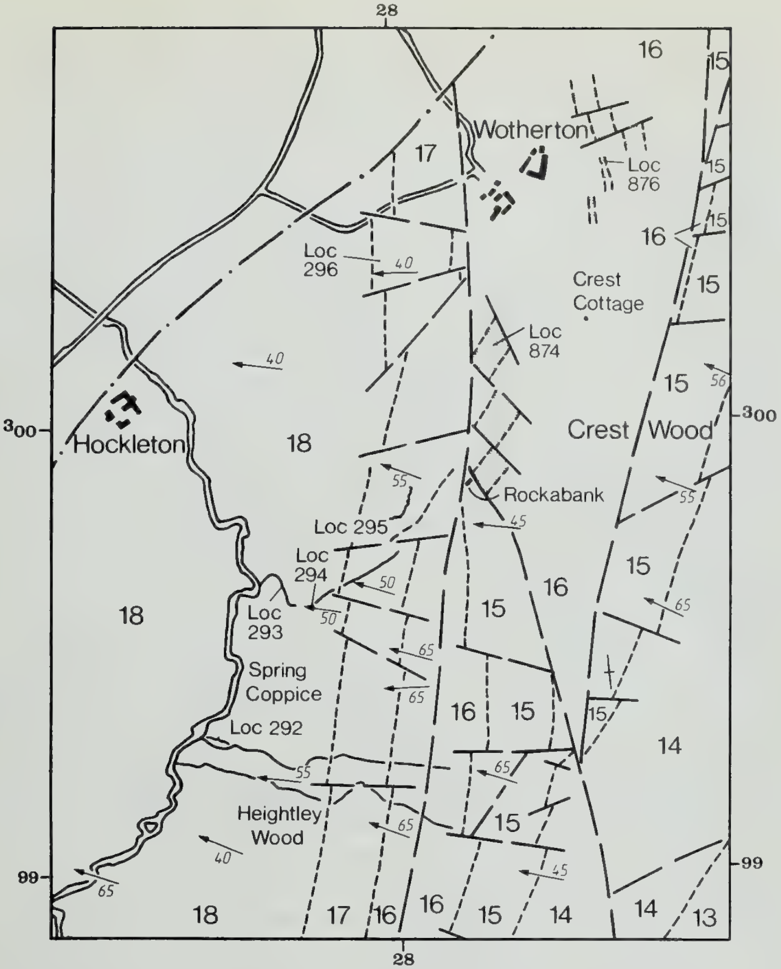
28
16
15
Wotherton
17
Loc 876
Loc 296
40
Crest Cottage
Loc 874
300
Hockleton
18
Crest Wood
56
Rockabank
55
Loc 295
45
Loc 294
50
Loc 293
65
Spring Coppice
Loc 292
14
Heightley Wood
99
13

Fig. 34 Geological map of the area south of Wotherton and NE of Chirbury. Adjoins Fig. 29. 13 = Spy Wood Member; 14 = Aldress Member; 15 = Hagley Volcanic Member; 16 = Hagley Shale Member, including tuff beds (dotted); 17 = Whittery Volcanic Member; 18 = Whittery Shale Member. (SO 29, SJ 20)

Hagley Shale Member

First usage. As Hagley Shales by Lapworth & Watts (1894 : 340, 342), a term which has since remained in almost constant use.

Type locality. No specific section was designated, though the general vicinity of Hagley farm, a mile (1·6 km) SE of Chirbury was presumably intended. The subject is discussed in more detail below.

Descriptive notes. Whittard (1931 : 333; 1960 : 144) described the strata briefly as 'rusty-weathering, bluish shales, with harder olive-green shales tending to be nodular'. At that time they had not yielded fossils but a few have now been found (see p. 54). The thickness was said to be of the order of 1000 ft (305 m).

Much of the neighbourhood of Wotherton village (Map and Fig. 34) is underlain by rocks of the Member but whereas outcrops of shales and flagstones are rare here, bands of tuffs and agglomerates within the shales are more resistant and, consequently, available for examination.

In particular a thin band of coarse agglomerate was seen in the sides of the road (Loc. 876) leading to Rorrington, *c.* 600 ft (183 m) ENE of Wotherton. About 1200 ft (366 m) south of Wotherton (Loc. 874) are exposures of volcanics which are unusual in that the surfaces show what appears to be flow banding; if this is correctly interpreted, then we are dealing with one of the few lavas known from the area.

At Loc. 340 in the stream-section 1250 ft (381 m) at 084° true from Marrington farm (Fig. 32, p. 48) nearly all the succession, apart from one short length covered by felled trees, is visible. Whittard's notes did not specify this as type section for the Member, but it might be used as at least a supplementary type section. The rocks comprise bluish-grey hearted, greenish-grey weathering shales which on the outside are altered to a yellowish brown. Some are soft and contain little mica. Interbedded with the shales, and dominant in the lower part of the succession, are greenish-grey weathering, flaggy micaceous siltstones; less commonly there are more arenaceous, light grey flags. A striking feature of all these rocks is the general paucity of fossil remains, and the most abundant specimens so far found are from interbedded tuffs. In most respects the rocks of the Hagley Shale Member are comparable with those of the Whittery Shale Member and clearly belong to the same deposition, the Hagley and Whittery Volcanic Members representing short-lived episodes of vulcanicity which nevertheless resulted in a considerable thickness of deposits. The more westerly outcrops (Loc. 339) of the Shale Member in this stream section are deeply-weathered, friable shales in which amplexoid-like graptolites have been found. Between these rocks and the main section is a large bed of tuff (Loc. 362) *c.* 7 ft (2·13 m) thick, with some interbedded shales.

Further exposures of the Hagley Shale Member are seen in the vicinity of the River Camlad both NE and SE of Calcot (Fig. 32, p. 48). At Loc. 746 a presumably interbedded tuff shows occasional graptolites in relief and contains the trinucleid trilobites *Broeggerolithus broeggeri* (Bancroft) and *Salterolithus caractaci* (Murchison), indicating a Caradoc, Lower Soudleyan age. A good section in the lane immediately NE of Alport (Loc. 744) shows 130 ft (39·6 m) of shales (Fig. 30, p. 44) with flagstone beds dipping approximately 50° at 290° true. Nearly 30 bands of flags occur, ranging from an inch (2·5 cm) to a foot (30 cm) in thickness and totalling some 6 ft (1·83 m). A small shelly fauna again indicates a Lower Soudleyan age. Whittard's notes suggest that the section might well be ranked as a type section for the Member.

Shales of the Member crop out intermittently along the Chirbury road just outside the village of Church Stoke (Fig. 35), particularly at Loc. 742, 1550 ft (472·4 m) north of St Nicholas' church. The exposure there includes several beds, up to 2 in (5 cm) thick, of tuffaceous flags, horizons which suggest that the volcanics of the succeeding Member are being anticipated. Within Church Stoke village, the road section 500 ft (152·4 m) at 323° true from St Nicholas' church (Loc. 739) shows rusty-weathering, greenish-grey, micaceous shales with thin, seldom more than 2 in (5 cm) bands of micaceous flags, beds which yielded *B. broeggeri* and *S. caractaci.* Loc. 738, 400 ft (122 m) at 212° true from St Nicolas' church, shows greenish-grey, micaceous flags and shales which constitute the last exposure of the Hagley Shale Member before glacial deposits forming the southern boundary of the Inlier are reached.

Whittery Volcanic Member

First usage. As Whittery Ashes, by Lapworth (1887 : 662). The name was listed in a stratigraphical table and no further details were given.

Type section. According to Whittard (1960 : 283) it is 'quarry in Marrington Dingle, east of Whittery, west Shropshire'. This appears to be a misprint because no such quarry exists east of the farm named Whittery, and Marrington Dingle lies to the south of both Whittery and Whittery Wood. It seems likely that the intended type section was the one in Whittery Quarry, just over a quarter of a mile (0·4 km) SSE of Whittery and at the southern end of Whittery Wood. There only the upper portion of the volcanic member is exposed, together with the basal part of the succeeding Whittery Shale Member (see p. 59).

Descriptive notes. Published descriptions of the Whittery volcanic rocks are both few and brief. Lapworth's introduction of the term in 1887 gave no description. Lapworth & Watts (1894 : 316,

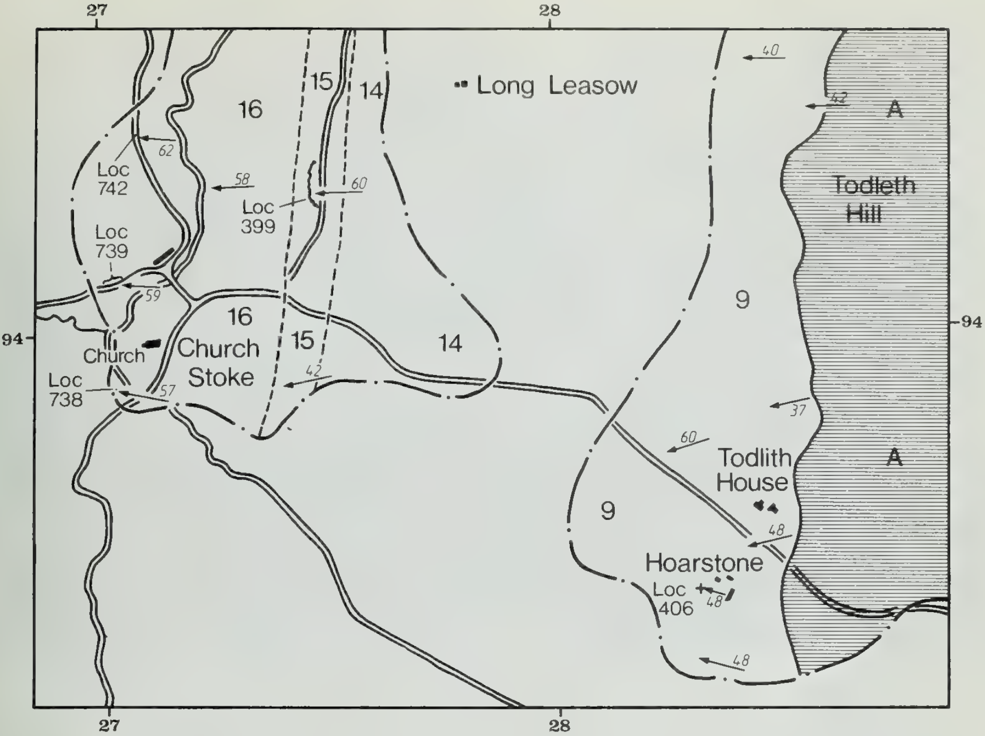

Fig. 35 Geological map of the area between Church Stoke and Todleth Hill, in the SW corner of the Shelve Inlier. 9 = Weston Member; 14 Aldress Member; 15 = Hagley Volcanic Member; 16 = Hagley Shale Member; horizontally shaded outcrop A – andestic intrusion of Todleth Hill. (SO 29)

318–319) noted the rocks as 'Whittery Ash' and listed them in a stratigraphical table. They cited Whittery Quarry and Walk Mill Quarry (presumably the quarry *c.* 450 ft (137 m) SE of Walkmill; Fig. 33, p. 52) as being places where the beds were 'splendidly exposed'. The volcanics were said to consist of 'andesitic and rhyolitic breccias and conglomerates, fine ashes with curious spherulitic or pisolitic structures, and bands of shale often fossiliferous'. Beds showing ripple markings were also recorded.

Whittard (1931 : 333) stated merely 'The Whittery Volcanic Group repeats the general lithological and petrological characters shown by the rocks of the Hagley Volcanic Group'; later (1952 : 164) he noted the rocks only briefly and gave the thickness as 300 ft (91·5 m). Subsequently (1960 : 283) he described them briefly as 'crystal and lithic tuffs, agglomerates and breccias with thin interbedded shales. Thickness 300 ft.'

The northernmost outcrops of the Whittery Volcanic Member occur in the vicinity of Wotherton (Fig. 34, p. 53), where part of the outcrop is faulted against the Hagley Shale Member to the east and the beds, which dip 40° bearing 280° true, were once quarried at Rock Coppice (Loc. 296). The nature of the junction between the Whittery Volcanic and Shale Members at this locality is noted in more detail under the description of the latter Member.

Of particular interest in this district is the outcrop 500 ft (152 m) SW of the house called Rockabank, 2250 ft (686 m) south of Wotherton (Fig. 34). At this point (Loc. 295) there occurs what Whittard described as an 'amazing development' of volcanic agglomerate with boulders up to 3 ft (0·9 m) in diameter, though most are half that size or smaller, in a matrix of coarse lithic tuff (Fig. 37). Those blocks which were examined showed the rock to be a lava, possibly a hornblende andesite, and the boulders are so numerous, and in places so tightly packed together,

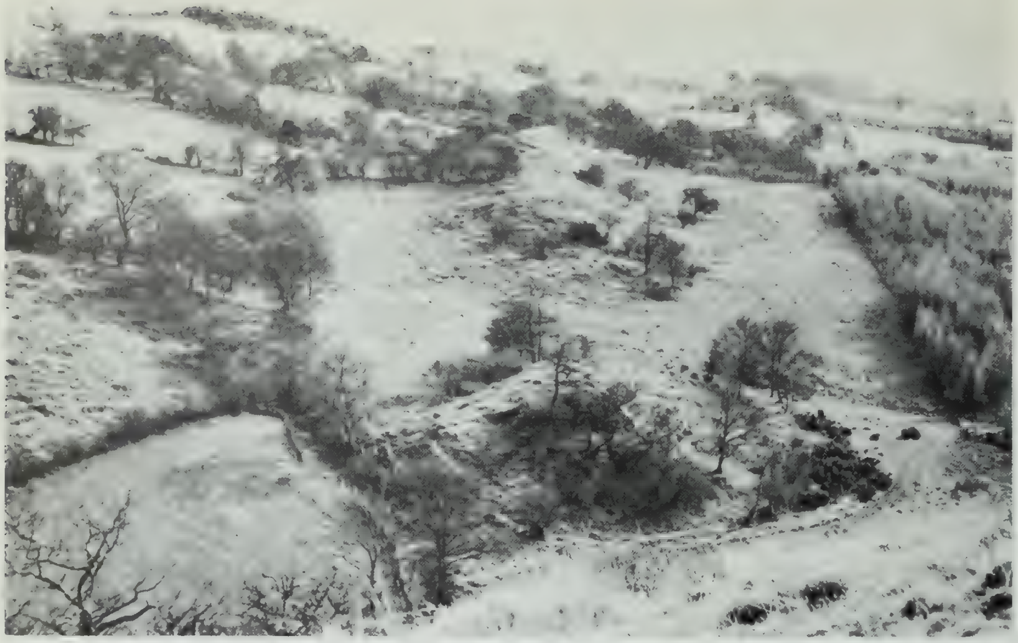

Fig. 36 Topography of ridges formed by Whittery Volcanic Member, here faulted, with intervening hollows excavated in regressive, interbedded shales. View looking south from Rockabank, 600 yd (550 m) south of Wotherton, towards Heightley Barn, 600 yd (550 m) NE of Whittery.

that the matrix is not easy to find. There is no evidence, either north or south of the Rockabank outcrop, of volcanic material which approaches this agglomerate in coarseness, though good outcrops of agglomerate showing fragments up to 3–4 in (75–100 mm) occur nearby. The question remains: have we at last a focus for part of the Caradoc vulcanicity in the Shelve Inlier? Mapping fails to show that the rock is in the form of a neck, although the general shape of the outcrop tends to suggest this. On the other hand, the rock appears to be interbedded; but here one should remember that, assuming the neck was originally vertical, the sides of the neck would now be approximately at 45°.

The volcanic rocks of the Whittery Volcanic Member in this area form a feature which runs SSW, its position 'stepped' by intermittent dip faults, but occasional indentations run along the strike owing to differential erosion of shale beds in the sequence, and it is clear that not inconsiderable masses of shale occur interbedded in the marine volcanics. On a hillside such as the east side of Marrington Dingle (Fig. 32, p. 48), where the top and bottom of the Volcanic Member can be mapped with reasonable confidence, shale fragments have been brought to the surface by rabbits at several points mid-way up the slope. A shale depression was mapped north of Heightley New Barn, 1650 ft (503 m) NE of Whittery, and may represent a similar condition appearing farther south (Fig. 33, p. 52).

The large quarry (Loc. 299) at the southern end of Whittery Wood (Fig. 33) is the original Whittery Quarry and therefore the probable type section for the Volcanic Member, the rocks of which were once extensively quarried there. The section shows also part of the overlying Whittery Shale Member, the beds of which include flags and bands of volcanic rocks, indicating waning vulcanicity as at Loc. 296 (see p. 59). Some of the bands may be up to 2 ft (0·61 m) thick and one may once more appreciate the possibility of misidentifying such rocks as part of the Volcanic Member when seen in isolated exposures. Six hundred feet (183 m) to the south is a smaller quarry (Loc. 875), almost certainly the Walk Mill Quarry of Lapworth & Watts (1894 : 318), which shows

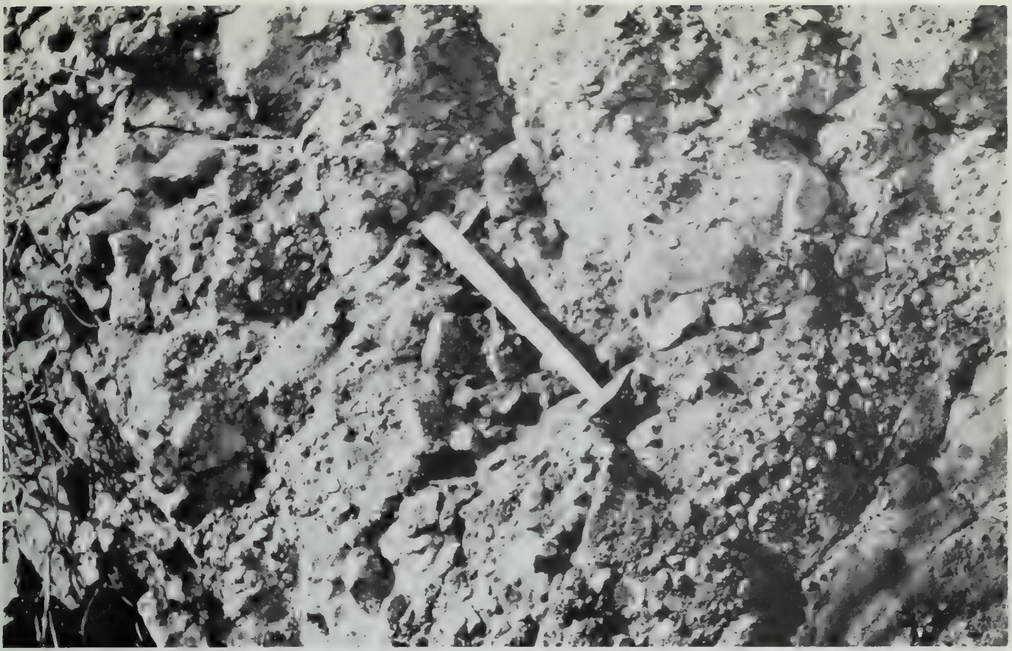

Fig. 37 Volcanic agglomerate in Whittery Volcanic Member at Rockabank, 600 yd (550 m) south of Wotherton, 1·9 miles (3 km) NE of Chirbury.

normal volcanics but is of interest because at the top there is a band showing flow-casting on its lower surface, where it rests on shale.

Four hundred feet (122 m) south of Walk Mill Quarry a variety of tuffs, both lithic and the so-called 'throstle-breasted', is shown (Fig. 33, p. 52) in a small disused quarry (Loc. 358), 300 ft (91·4 m) SE of which is a hillock where good exposures (Loc. 337) of agglomeratic tuff are found, with well-rounded boulders, some attaining a length of a foot (30 cm). Northwards the agglomeratic character of the rock remains evident but the agglomerate is obviously interbedded with crystal and lithic tuffs. The hillock is peculiar in that it is followed to the west by a flat region before the steep flank of Marrington Dingle is reached, and it is not clear whether one is dealing with an isolated outcrop or one that is faulted from the main outcrop of Volcanic Member. The hillock is separated by a small valley from the outcrop of Volcanic Member as traced from the north and it strikes southwards into open country.

Good examples of agglomerate occur a little farther south on another hillock (Loc. 338) upon which Bank Farm, 900 ft (274 m) east of Marrington Hall (Fig. 33) is built. This should not be confused with the building called Bank which is situated 1060 ft (323 m) SE of Whittery (Fig. 33).

The faulting of the Whittery Volcanic Member in the area parallel to Marrington Dingle and south of Whittery Wood is noteworthy because, by the usual methods of determination, the downthrow is to the north. However, if the upper surface of the volcanics is traced in relation to its O.D. level, the fault block to the south is at a lower level than its fellow to the north, so that the downthrow is apparently to the south. It would appear that the south side is really the downthrow, but that tear-faulting has resulted in a greater horizontal than vertical movement. Consequently the horizontal shift (to the east on the north side of each fault) is greater than the displacement due to a southerly downthrow.

At a point 210 ft (64 m) ENE of the building called Marrington (Fig. 32, p. 48), the east bank of the River Camlad is intersected almost at right angles by an unnamed stream,the upper reaches of which show an almost continuous section (Locs 360–1) through the Whittery Volcanic Member.

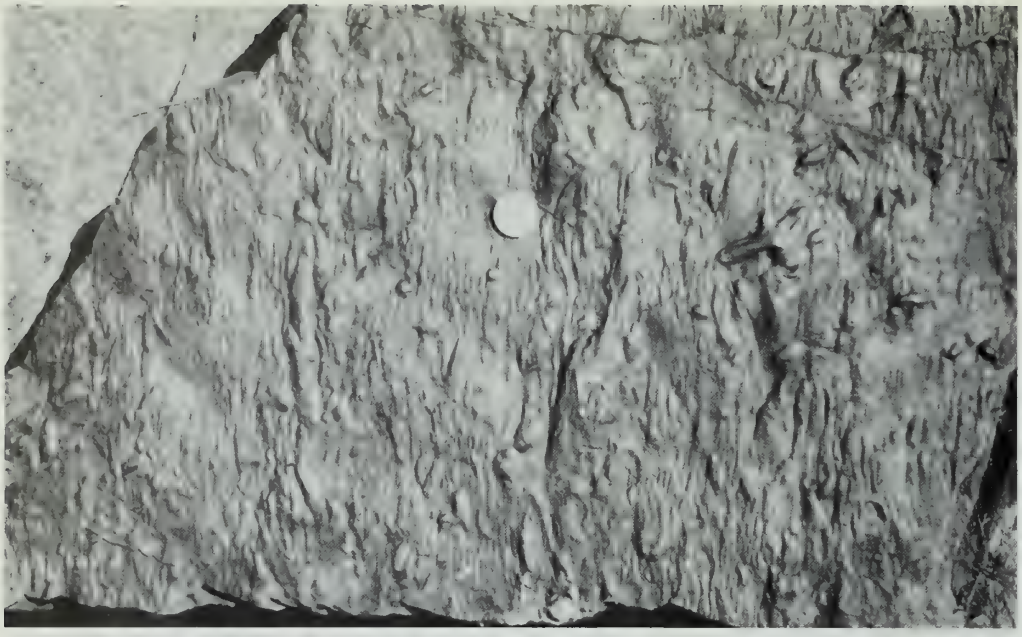

Fig. 38 Flow casts in Whittery Volcanic Member. Quarry 220 yd (200 m) south of Whittery Quarry, 0·83 mile (1·34 km) east of Chirbury. (Coin 28 mm diam.)

The stratigraphically lower half of the sequence (Loc. 361) contains much more shale than the higher half and the tuffaceous rocks are much finer grained, some of them yielding graptolites. At this point volcanics seen just above a bed of shale $1\frac{1}{2}$ ft (46 cm) thick occur in large, concretionary masses which are pillow-shaped, concentrically banded and a minimum of 4 ft (1·22 m) in diameter. These are demonstrably depositional and not tectonic structures. Some anomalous easterly dips seen a little farther upstream may indicate strike faulting and folding, thought to be of a very minor character.

Farther SW, 440 ft (134 m) SE of Marrington, a section (Loc. 363) in the Camlad shows a slight anticlinal flexure whereby volcanics near the top of the Member occur in the river and are succeeded by beds of the Whittery Shale Member, seen in the west bank only a short distance south.

The southernmost outcrops of the Whittery Volcanic Member are seen at an old quarry (Loc. 747; Fig. 32, p. 48) just north of Calcot and by the west bank of the Camlad. A minor syncline is developed there and the rocks, which include tuffs interbedded with shales at the eastern end of the quarry, are much broken. Southwards beyond this point the outcrops are obscured by glacial deposits.

Whittery Shale Member

First usage. By Lapworth & Watts (1894 : 316, 319). The name was listed as Whittery Shale in a stratigraphical table and as Whittery Shales in the text, but no description was given.

Type locality. None was designated by Lapworth & Watts, though the beds were said to 'form the ground between Marrington and Chirbury'. The base of the Member is seen at Whittery Quarry (see p. 56).

Descriptive notes. The rocks of the Whittery Shale Member resemble those of the Hagley Shale Member, and comprise predominantly blue-grey, micaceous shales which appear light rusty brown or olive-green after weathering. Other, but subsidiary, rock-types include bluish green, heavily micaceous, flaggy bands and both fine- and coarse-grained interbedded tuffs. The tuffs in particular are liable to be found fossiliferous, with both shelly and graptolitic faunas.

Whittery Quarry (Loc. 299), at the southern end of Whittery Wood, near Chirbury (Fig. 33, p. 52), exhibits the boundary of the Whittery Shale Member with the underlying Whittery Volcanic Member. The rocks there dip 45° bearing 292° true and show flags and volcanic bands interbedded with the shales. One important feature there is that within the shales there may be bands of volcanics up to 2 ft (0·61 m) thick, and small, isolated exposures of such rocks might lead one to map such outcrops mistakenly as the Whittery Volcanic Member.

The junction between the Volcanic and Shale Members is seen also in the western part of the old quarry (Loc. 296) at Rock Coppice, 333 yd (305 m) SW of Wotherton (Fig. 34). Above the massive tuff there are alternations of thin tuff, mostly 1 in (25 mm) but at maximum 2 in (51 mm) thick, and shales up to 6 in (152 mm) thick, totalling about 6 ft (1·83 m), after which point normal shale conditions became established. The junction between the two members is thus a normal one, with a gradual passage from volcanics to shale, demonstrating that the end of the vulcanicity was marked by a few, probably explosive, eruptions. This was the last of the vulcanicity in the Ordovician of west Salop except for tuffaceous bands at several levels in the Whittery Shale Member, indicating short and unimportant recrudescences in the vulcanicity.

Streams flowing westwards into the River Camlad and down the dip of the Whittery Shale Member show almost continuous sections at points 2600 ft (792 m) NE (Loc. 292) and *c*. 3800 ft (1158 m) NNE (Loc. 293) of Heightley (Figs 33–34), near Chirbury. The predominant rock type is shale but bands of flagstone are developed; a peculiar and so far characteristic rock is a tuffaceous shale which contains stony fragments up to half an inch (13 mm) in diameter. The latter rock type occurs also at Loc. 294, *c*. 250 ft (76 m) SE of, and upstream from, Loc. 293, and has yielded fossils which include *Salterolithus caractaci* (Murchison) and *Broeggerolithus broeggeri* (Bancroft), characteristic of the Glenburrell Beds (Lower Soudleyan) of the Onny Valley in SE Salop.

Beds high in the Shale Member crop out along the stream south of Chirbury at Locs 272 and, especially, 273 (Fig. 33, p. 52). The latter shows a good section in which shale is the predominant element though there are some flaggy layers. A few graptolites have been obtained from this locality.

The most westerly exposure of the Ordovician rocks of the Shelve Inlier occurs at Loc. 752, a quarter of a mile (0·4 km) NE of Trimberth. Thirty years ago the strata of the Whittery Shale Member were better exposed there than nowadays but the lithology is typical and there is no mistaking their age. Of passing interest there is a small quarry where the shales are no longer exposed but could be examined thirty years ago; on that occasion the dip was found to be high and to the SE. The significance of this change-round from a prevailing westerly dip cannot be determined as there are no other exposures in the immediate neighbourhood, where the only material to be seen is the ubiquitous boulder-clay.

Miscellaneous notes

Correlation with neighbouring Ordovician successions

The correlation of the Shelve Ordovician rocks with those of the Caradoc District, the Breidden Hills and the Pontesford district was summarized by Whittard (1952 : table III) in a table which listed the corresponding graptolite zones. The Stiperstones Member and Mytton Member were equated with the combined *Didymograptus extensus* and *D. hirundo* Zones; the Hope, Stapeley Volcanic, Stapeley Shale and Weston Members with the *D. bifidus* Zone; the Betton Member with the *D. murchisoni* Zone; and the Meadowtown Member questionably with the *Glyptograptus teretiusculus* Zone. The Rorrington Member was equated with the *Nemagraptus gracilis* Zone and part of the *Diplograptus multidens* Zone; the Spy Wood Member questionably with part of the *D. multidens* Zone; and the Aldress Member with part of the *D. multidens* Zone and part of the *Dicranograptus clingani* Zone; the remainder of the succession was equated with part of the *D. clingani* Zone and the *Pleurograptus linearis* Zone.

The problem of how to account for this supposed correlation of the highest Ordovician strata of the Shelve Inlier troubled Whittard for several years and appears to have arisen from the Geological Survey's discovery of graptolites in tuffs of the Hagley Volcanic Member at the type locality of Hagley Quarry. This find was reported by Whittard (1931 : 334) and the specimens, identified by G. L. Elles, were interpreted as indicating 'a horizon about the base of the Zone of *Pleurograptus linearis* or at the very top of the Zone of *Dicranograptus clingani*'. However, it had for some years been customary to regard the Shelve Ordovician rocks as constituting a virtually complete succession. For example, Watts (1925 : 340, 343) placed the top of the Caradoc Series immediately above the Whittery Volcanic Member and regarded the Whittery Shale Member as possibly representing the Ashgill. Consequently no major policy change was required in order to relegate the Whittery Shale Member to a slightly lower horizon, supposedly in the highest Caradoc Series.

Correlation of the Shelve rocks of Caradoc age has been facilitated by use of the 'shelly' zones and stages established by B. B. Bancroft, though their original application was often inaccurate and only relatively recently has a more convincing picture emerged. Bancroft's (1933) correlation tables followed the previous practice (e.g. Lapworth & Watts 1894 : 316) of equating the Hoar Edge Grits of the Caradoc district with the Spy Wood Member (then Spy Wood Grit), claiming that the latter contained '*Marrolithus* (Costonian type)'. Whittard's (1966 : 281) later discovery of the South Salop Costonian index trilobite *Costonia ultima* (Bancroft) – a species originally assigned to *Marrolithus* – in the Spy Wood Member (see p. 50) showed this part of Bancroft's table to be essentially correct, though it had probably been made for the wrong reasons, as Bancroft never recorded any South Salopian species from the Shelve Costonian and his collection contained no such material. Bancroft did record a trinucleid assemblage of *Broeggerolithus broeggeri* (Bancroft) and *Salterolithus* from the Hagley Shale Member as being indicative of the Soudleyan Stage, to which subdivision he also assigned the Whittery Volcanic Member, but the remainder of his succession showed the Whittery Shale Member ranging in age from Soudleyan to Onnian and he did not recognize that most of the Caradoc Series is missing from the Shelve Inlier.

Some of Whittard's 1952 conclusions were subsequently revised by him and in the first part of the Shelve trilobite monograph (Whittard 1955 : 5) the Whittery Volcanic and Shale Members were said to extend no higher than the *D. multidens* Zone and, questionably, the basal *D. clingani* Zone, a conclusion more in keeping with evidence from the Caradoc Series of the type area. In a later part of the monograph (Whittard 1966 : 297) both the Betton Member and the underlying Weston Member were placed in the *D. murchisoni* Zone, thus reverting to a correlation suggested much earlier (Whittard 1931 : 331).

Correlation of the shelly and graptolitic faunas in the Llandeilo and lowest Caradoc Series proved difficult and Whittard's (1966 : 298) final published pronouncement differed from his earlier interpretations, particularly with reference to the boundary between the Meadowtown and Rorrington Members and the stratigraphic value of such trilobites as *Lloydolithus lloydii* (Murchison). The latter was shown to be confined to the Meadowtown Series which, in turn, had previously been equated with the whole of the Llandeilo Series and the *Glyptograptus teretiusculus* Zone. More recent work on the Ordovician of south Wales by Addison (*in* Williams *et al.* 1972 : 35–36) clarified the situation by showing that the Meadowtown Member, with its abundant and characteritic *L. lloydii*, corresponds only to the Lower Llandeilo of the type area, and demonstrated that the base of the *Nemagraptus gracilis* Zone must be extended downwards to include, at least approximately, the Middle and Upper Llandeilo Series. We may note here that a revision (Dean 1967: 317–319) of the correlation between the Caradoc stages and corresponding graptolite zones placed the highest Costonian of the Caradoc in the *D. multidens* Zone by analogy with the Shelve succession, while the underlying Costonian strata contain a shale band yielding *Nemagraptus gracilis*. At Shelve the Spy Wood Member, at least partly Costonian in age, is underlain by shales of the Rorrington Member, a subdivision said by Whittard (1955 : 5) to include both the *N. gracilis* and *D. multidens* (in part) Zones, so that correlation of shelly and graptolitic faunas in this part of the succession is not yet precisely defined.

The Ordovician rocks of the Breidden Hills, *c.* 9 miles (14·5 km) NNW of Shelve, were described by Watts (1925 : 340, 343) and later by Wedd (1932), who erected a number of local lithostratigraphic names, some of which may represent strata duplicated by faulting. The relatively restricted succession commences with a series of 'Lower Shales', base not seen but thickness at least 1770 ft (540 m), which are known also as Nemagraptus Shales as they contain the eponymous genus and other graptolites suggesting an assignment to the *N. gracilis* Zone, and thus to the lowermost Caradoc or Middle/Upper Llandeilo Series. The shales are succeeded by the so-called 'Black Grit', a flaggy, black sandstone 20 ft (6 m) thick which corresponds in position approximately to the Spy Wood Member of Shelve and part of the Hoar Edge Grits of the Caradoc district. The sandstone is followed by a sequence 1870 ft (570 m) thick comprising flags and shales with two groups of volcanic rocks, which proved partially fossiliferous and from which Standring (Dean *in* Williams *et al.* 1972: 41) obtained the Lower Soudleyan trilobites *Broeggerolithus broeggeri* and *Salterolithus caractaci.* This record confirms to a large degree Watts' (1925 : 343–344) correlation of the Breidden volcanics with the Hagley and Whittery rocks of Shelve, though Whittard (1952 : table 3) at one time regarded them as being somewhat older.

Only three-quarters of a mile (1·2 km) east of the north end of the Shelve Inlier lies the small, isolated area of Ordovician rocks beside the eastern flank of Pontesford Hill (Map). Redescribed by Dean & Dineley (1961), these are known now to include a basal conglomerate which rests with marked unconformity on Pre-Cambrian (Uriconian) rocks and is followed successively by grey shales with *Diplograptus multidens* and then grey-green mudstones containing both graptolites of the *D. multidens* Zone and trilobites of the Lower Soudleyan Stage. These last two sets of strata correspond respectively to the Harnage Shales *sensu stricto* of the northern Caradoc district and the Glenburrell Beds of the Onny Valley. The rocks bear a remarkably close resemblance to those of the Caradoc district but not to those of the Shelve Inlier, from which they are separated by an important structural line—the Linley–Pontesford Fault—and it is this fault-system rather than the Church Stretton fault-system which marks the most profound change in development of the Ordovician rocks in Salop (Dean 1964 : 37; *in* Williams *et al.* 1972 : 39).

Intrusive igneous rocks

Lapworth & Watts (1894 : 337–343) divided the igneous rocks of the Shelve Inlier into two groups, namely 'the interbedded andesitic ashes and lavas of Arenig and Bala ages and the intrusive dolerites and picrites'. The latter, both dykes and sills, were said to consist chiefly of hypersthene dolerite and were described as being of post-Llandovery age as they 'come into contact with and somewhat alter the *Pentamerus* limestones'. This last view, reiterated by Watts (1925 : 335), was subsequently shown by Whittard & Blyth (*in* Blyth 1944 : 178) to be untenable and the Shelve volcanics and intrusives are generally accepted as predating the local Upper Llandovery strata. In a very brief account Watts (1905: 177) noted that the Shelve vulcanicity occurred in two maxima (one of Arenig, one of Bala age) and that the rocks were 'almost exclusively andesites in the form of lavas and tuffs', some of which were said to be fossiliferous, having been deposited under marine conditions. The last stages of the vulcanicity were stated to have been 'marked by the intrusion of sills, laccolites and dykes, along surfaces of movement due to folding, faulting and torsion'. A later description by Watts (1925 : 341–343) placed the two principal volcanic outbursts in the Llanvirn (Stapeley Volcanic Member) and Caradoc (Hagley and Whittery Volcanic Members), and the water-deposited andesitic tuffs and ashes of the former were stated to have been 'invaded by massive sills of andesite and by dolerites of the Llanfawr type as well as by the normal type'.

The principal paper dealing with this aspect of the Shelve Inlier is that of Blyth (1944), who showed that the basic intrusions, ranging from picrite to alkali-rich andesite, formed a single co-magmatic suite having affinities with rocks of plateau-basalt or olivine-basalt type. Some of Blyth's work was carried out in collaboration with Whittard and the results of his mapping of the dolerites of Squilver Hill and Corndon Hill, as well as of several smaller intrusives and dykes, is evident in the present work, though some of the geological boundaries were subject to later, minor revision. Watts (1925 : 354; *in* Whittard 1931*a* : 340) had earlier expressed the view that the Corndon intrusion was 'a laccolite intruded along an anticline which has sagged in the middle', an interpretation modified slightly by Blyth (1944 : 178–183; see also Whittard 1952 : 164), who considered the rock to be 'a faulted phacolith' intruded into the crest of a pre-existing anticlinal axis and having a thickness not necessarily more than *c.* 200 ft (61 m).

Although almost all Whittard's notes on the igneous intrusives are confined to brief field observations, a somewhat longer section deals with the andesite of Lan Fawr (Map and Figs 23, p. 34; 24, p. 36). The outline of the andesite, which appears to show little petrological variation, was mapped in detail and a surprising feature is that the shales into which it is intruded are little altered, show no spotted condition, and are at the most only slightly indurated. This andesite therefore has less effect on the country rock than the Corndon dolerite and many of the minor doleritic intrusions, which convert the rock at least into an adinole. The other feature which emerged gradually during mapping is the post-faulting age of the andesite. No faulted outcrop of the andesite can be proved, and yet well-established faults in the local sedimentary rocks trend towards the andesite and might well emerge on the other side. If this claim is justified, and no other answer has been found to explain the outcrops of the sedimentary rocks, the intrusion of the andesites was probably almost the last phenomenon to occur in the Ordovician history of the inlier. Certainly dolerites were intruded along fault planes but some, such as that of Corndon, are evidently cut by faults. The dolerites may thus be claimed as approximately equivalent in age to most of the faulting, though sometimes slightly older and often slightly younger. The andesite, however, is unaffected by faulting and there is no known case where andesite and dolerite are in juxtaposition. Nevertheless, the Lan Fawr andesite is jointed, and in places shattered, by tectonic events of uncertain age but almost certainly pre-Upper Llandovery. Excluding tectonics, there is a certain amount of mineralization with galena and this mineralization may be the last Ordovician event of which we have any record, the intrusion of the andesite being the penultimate one.

Silurian rocks

The stratigraphy and distribution of the Llandovery rocks in South Salop were the subject of early researches by Whittard whose 1932 account gave maps and descriptions of the outcrops around the Shelve Inlier. A review by Ziegler *et al.* (1968 : 742) introduced three new lithostratigraphic names (Bog Quartzite, Venusbank Formation and Minsterley Formation) for Whittard's more generalized terms and claimed that their 'only major re-interpretation' of his work had been to connect the so-called 'Venusbank outlier' (Whittard 1932 : pl. 61A) with the large outcrops lying to the north in the Hope Valley. During his later mapping of the area Whittard had, in fact, come to the same conclusion and a revised boundary for these Silurian rocks at Venusbank was published by him (1955 : fig. 1) as part of an outline map of the Shelve Inlier which matches that of the present work (Fig. 15, p. 25), though he did not draw attention to the fact. A further minor modification, described on p. 272 of the manuscript notes, involved the outlier of Silurian rocks at Round Hill, 1900 ft (579 m) WSW of Tankerville Mine. The small area described originally by Whittard (1932: 878, fig. 2) was subsequently extended, particularly to the NW, and the revised boundary is shown in the Map.

The several outliers approximately centred on Ritton Farm (Fig. 22, p. 33) are difficult to map in detail and the indication of a particular outline is adduced from the abundance of flags of sandstone which are unmistakable. In some cases there may be no solid rock left as a cap to the hill, but the very presence of a marked hill composed of soft shale is indicative of a protective covering which is still retained or has been removed only recently.

Geological structure of the Shelve Inlier

Perhaps the most obvious structural features of the inlier are the Ritton Castle Syncline and, immediately to the west of it, the Shelve Anticline. The axes of both these folds run approximately NNE and in general the regional strike of the Ordovician members follows suit. The existence of these structures has long been appreciated and was noted by Lapworth & Watts (1894 : 314, 317) whose then unpublished map (used later *in* Pocock & Whitehead 1948 : pl. 11) shows them clearly. A later account by Watts (1925 : 343) stated: 'In addition to this folding [the syncline and anticline] the rock structures are often cut by faults, the more important of which are longitudinal but tend to swing across the strike'. He noted that 'combined folding and faulting has produced remarkable outcrops in the Stapeley Stage at Bromlow Callow and the Hagley Stage near Wotherton', and observed that the faults often coincided with dolerite and picrite intrusions or, in the case of small transverse faults, with mineral-bearing lodes.

Unfortunately the Whittard manuscript notes contain no comprehensive account of the geological structure, allusions to which are confined to a few scattered comments. However, some of Whittard's main conclusions were expressed in his *A geology of South Shropshire* (1952 : 185–189), in which paper he noted particularly the 'powerful northerly-trending tear-faults which were accompanied by complementary shears running not quite at right-angles to one another and each making an angle usually in excess of 45 degrees with the main tear-faults'. Whittard considered that his recognition of the tear faults (which may readily be seen in the Map) provided the main difference between his and earlier interpretations of the structure of the Inlier. Examination of his map shows that a few of the tear faults coincide approximately with less extensive dislocations shown on the map of Lapworth & Watts (*in* Pocock & Whitehead 1948 : pl. 11), and it is likely that the latter structures are the longitudinal faults noted by Watts in 1925 (see p. 62). The main folding and faulting were ascribed by Whittard (1952 : 186–187) to the Taconian Orogeny and are certainly of pre-Upper Llandovery age. As far as the Shelve Inlier is concerned, they are no older than the Soudleyan Stage of the Caradoc Series, and may well be post-Caradoc in view of the lack of evidence for disturbances of this magnitude up to the top of the Onnian Stage in southeast Salop.

One can really only confidently determine the northerly-trending tear fault pattern by being able to feel sure of the relative stratigraphical ages of beds of somewhat similar but not identical lithologies when they are brought into juxtaposition; for example, Aldress, Rorrington, Meadowtown and Betton Members and some beds of the Weston Member. Although by no means the same, their lithologies in small exposures may be similar enough to cause much indecision regarding which subdivision they belong to. Consequently knowledge of the faunal sequence was of great importance in confirming the lithostratigraphic assignment of many localities. The more obvious faults are the complementary shears because they run across the strike, displacing ridges formed of hard rocks, instead of running with the strike as do the major tear faults, in regions occupied by softer rocks. Without the aid of stratigraphic palaeontology the pattern of faults developed through shear might well not have been recognized, with regard to the dominant northerly-trending members.

A major feature of South Salop geology, emphasized by Whittard (1952 : 185) and reiterated in a later review by Dineley (1960 : 6), is the large number of unconformities, often of major proportions, which range in age from Pre-Cambrian to Mesozoic. These are particularly noticeable in the Caradoc district, some 7 miles (11·3 km) to the east, where beds of only Caradoc age are found, resting with profound unconformity upon Pre-Cambrian rocks and succeeded unconformably by Upper Llandovery strata. As far as the Shelve Inlier is concerned, however, few breaks are documented. Following the probably relatively small disconformable gap between the Stiperstones Member and Shineton Shales (the base of which is not seen here), the Ordovician succession continued virtually unbroken, except by periodic outbursts of volcanic activity, from the Lower Arenig Series to the Lower Soudleyan Stage of the Caradoc Series. The Ordovician rocks of the Caradoc district were deposited along the margin of the so-called Midland Block and were separated by the line of the Linley–Pontesford Fault from the subsiding region farther west in which the Shelve rocks were deposited and which was connected with other areas of marine deposition in southern Europe, including especially Bohemia.

References

Bancroft, B. B. 1933. *Correlation tables of the stages Costonian–Onnian in England and Wales.* 4 pp., 3 tables. Blakeney, Glos. (privately printed).

Blyth, F. G. H. 1938. Pyroclastic rocks from the Stapeley Volcanic Group at Knotmoor, near Minsterley, Shropshire. *Proc. Geol. Ass.*, London, **49** : 392–404, figs 66–68.

—— 1944. Intrusive rocks of the Shelve Area, West Shropshire. *Q. Jl geol. Soc. Lond.*, **99** : 169–204, pl. 20.

Bulman, O. M. B. 1928. A monograph of British dendroid graptolites, **2** : i–xxxii, 29–64, pls 3–6. *Palaeontogr. Soc.* (*Monogr.*), London.

Callaway, C. 1878. On a new area of Upper Cambrian rocks in South Shropshire, with a description of a new fauna. *Q. Jl geol. Soc. Lond.* **33** : 652–672.

Dean, W. T. 1964. The geology of the Ordovician and adjacent strata in the southern Caradoc District of Shropshire. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **9** : 257–296, 2 pls.

—— 1967. Relationships of the Shelve trilobite faunas. *In* Whittard, W. F., The Ordovician trilobites of the Shelve Inlier, West Shropshire, **9** : 308–320, fig. 10. *Palaeontogr. Soc.* (*Monogr.*), London.

—— **& Dineley, D. L.** 1961. The Ordovician and associated Pre-Cambrian rocks of the Pontesford District, Shropshire. *Geol. Mag.*, London, **98** : 367–376, pl. 20.

Dineley, D. L. 1960. Shropshire geology: an outline of the tectonic history. *Fld Stud.*, London, **1** : 1–23, 10 figs.

Dines, H. G. 1958. The West Shropshire mining region. *Bull. geol. Surv. Gt Br.*, London, **14** : 1–43.

Earp, J. R. & Hains, B. A. 1971. *British Regional Geology. The Welsh Borderland.* (3rd ed.) xi+118 pp., 11 pls. London.

Hall, T. C. F. 1919. *Report on the Shropshire Mining District.* 35 pp., 3 tables. London (privately printed).

Harper, J. C. 1947. *Tetradella complicata* (Salter) and some Caradoc species of the genus. *Geol. Mag.*, London, **84** : 345–353, pl. 10.

James, J. H. 1956. The structure and stratigraphy of part of the Pre-Cambrian outcrop between Church Stretton and Linley, Shropshire. *Q. Jl geol. Soc. Lond.*, **112** : 315–337, pl. 15.

Lapworth, C. 1887. The Ordovician rocks of Shropshire. *Rep. Br. Ass. Advmt Sci.*, London, **56** (Birmingham 1886), C : 661–663.

—— 1916. In *Mem. geol. Surv. Summ. Prog.*, London, **1915** : 36–38, 3 figs.

—— **& Watts, W. W.** 1894. The geology of South Shropshire. *Proc. geol. Ass.*, London, **13** : 297–355, pls 8, 9.

—— —— 1910. Shropshire. *In* Monckton, H. W. & Herries, R. (eds), *Geology in the Field* (4): 739–769, pls 24, 25. London (Geologists' Association Jubilee Volume).

Pocock, R. W. & Whitehead, T. H. 1948. *British Regional Geology. The Welsh Borderland.* (2nd ed.) iv+80 pp., 11 pls. London.

——, ——, Wedd, C. B. & Robertson, T. 1938. Shrewsbury District, including the Hanwood Coalfield (One-inch Geological Sheet **152** New Series). xii+297 pp., 8 pls. *Mem. geol. Surv. U.K.*, London.

Salter, J. W. 1866. On the fossils of North Wales. *In* Ramsay, A. C., The geology of North Wales. *Mem. geol. Surv. U.K.*, London, **3** : 239–381, pls 1–26.

Stubblefield, C. J. & Bulman, O. M. B. 1927. The Shineton Shales of the Wrekin District: with notes on their development in other parts of Shropshire and Herefordshire. *Q. Jl geol. Soc. Lond.*, **83** : 96–146, pls 3–5.

Watts, W. W. 1905. On the igneous rocks of the Welsh Border. *Proc. Geol. Ass.*, London, **19** : 173–183, pl. 5.

—— 1925. The geology of South Shropshire. *Proc. Geol. Ass.*, London, **36** : 321–363, figs 26–40.

Wedd, C. B. 1932. Notes on the Ordovician rocks of Bausley, Montgomeryshire. *Summ. Progr. geol. Surv. Lond.*, **1931** (2) : 49–55, 1 fig.

Whittard, W. F. 1931. The geology of the Ordovician and Valentian rocks of the Shelve country, Shropshire. *Proc. Geol. Ass.*, London, **42** : 322–339, pls 10, 11.

—— 1931*a*. Easter Field Meeting (Extension) to Ministerley. April 8th to 11th, 1931. *Proc. Geol. Ass.*, London, **42** : 339–344.

—— 1932. The stratigraphy of the Valentian rocks of Shropshire. The Longmynd–Shelve and Breidden outcrops. *Q. Jl geol. Soc. Lond.*, **88** : 859–902, pls 58–62.

—— 1940. The Ordovician trilobite faunas of the Shelve–Corndon District, West Shropshire. Part I. Agnostidae, Raphiophoridae, Cheiruridae. *Ann. Mag. nat. Hist.*, London, (11) **5** : 153–172, pls 5, 6.

—— 1952. A geology of South Shropshire. *Proc. Geol. Ass.*, London, **63** : 143–197, 6 tables.

—— 1953. Report of Summer Field Meeting in South Shropshire, 1952. *Proc. Geol. Ass.*, London, **64:** 232–250, 1 fig.

—— 1955. The Ordovician trilobites of the Shelve Inlier, West Shropshire, **1** : 1–40, pls 1–4. *Palaeontogr. Soc.* (*Monogr.*), London.

—— 1958. Geology of some classic British areas: Geological Itineraries for South Shropshire. *Geol. Ass. Guide*, Colchester, **27** : 1–24, 14 figs.

—— 1960. England, Wales & Scotland. Ordovician. *Lexique Strat. int.*, Paris, **1** (3aIV) : 1–296.

—— 1960*a*. The Ordovician trilobites of the Shelve Inlier, West Shropshire, **4** : 117–162, pls 16–21. *Palaeontogr. Soc.* (*Monogr.*), London.

—— 1966. The Ordovician trilobites of the Shelve Inlier, West Shropshire, **8** : 265–306, pls 46–50. *Palaeontogr. Soc.* (*Monogr.*), London.

Williams, A. 1974. Ordovician Brachiopoda from the Shelve District, Shropshire. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) Suppl. **11** : 1–163, 28 pls.

—— ***et al.*** 1972. A correlation of Ordovician rocks in the British Isles. *Spec. Rep. geol. Soc. Lond.*, **3** : 1–74, 10 figs.

Ziegler, A. M., Cocks, L. R. M. & McKerrow, W. S. 1968. The Llandovery transgression of the Welsh Borderland. *Palaeontology*, London, **11** : 736–782, 14 figs.

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An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys. By the late W. F. Whittard, F.R.S. (Compiled by W. T. Dean)

Miscellanea

The Caradoc faunal associations of the area between Bala and Dinas Mawddwy, north Wales. By M. G. Lockley

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Miscellanea

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A new, possibly algal, microproblematicum from the Lower Carboniferous of England

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Synopsis

Hypocaustella cartimanduae gen. et sp. nov. is described from the Lower Carboniferous (Viséan D_1, D_2) of northern England. It consists of small monostromatic growths of calcareous-walled hexagonal-prismatic cells, with occasional larger rounded-lenticular cells. The evidence for its possible interpretation as an early coralline alga, and the evolutionary implications of this, are discussed.

Introduction

The little organism described below was discovered during examination for algae of two Viséan limestone samples. One is from the Great Scar Limestone of Ingleton, North Yorkshire; the other from the Oxford Limestone of Dunsall, Northumberland. The former is a biosparite with subordinate pyrites, rich in small foraminifera and microproblematica, with frequent ostracoda, occasional larger debris of brachiopods, bryozoa and serpulids, and rare fragments of the algae *Koninckopora* and *Ungdarella.* The other sample is also pyritic and foraminiferal.

Systematic description

Microproblematicum, incerta sedis

Genus ***HYPOCAUSTELLA*** nov.

Diagnosis. Small curved monostromatic growths of tiny hexagonal-prismatic calcified cells; growths presumed originally attached or partly encrusting, and sometimes showing branching; single larger rounded-lenticular cells occasionally present. Lower Carboniferous, Viséan D_1, D_2; northern England.

Type species. *H. cartimanduae* sp. nov.

Generic name. From a fancied resemblance of the cells to the hollow tiles of a Roman hypocaust or heating system.

Hypocaustella cartimanduae sp. nov.
Figs 1–7

Description. In numerous thin sections this organism appears as thin curved plate-like monostromatic growths, sometimes showing evidence of branching or division. All are under 1 mm in diameter, and a majority are 0·5 mm or less. None have been found attached to shell or other solid objects.

In vertical section the cells are square to high-rectangular. They vary in dimensions between one specimen and another, the smaller being square, the larger rectangular (Fig. 8). The basal calcification is usually well developed; the very thin lateral walls thicken at their outer terminations. An outer or upper calcification is only occasionally present, though the cells usually have a different crystalline infilling to that of the matrix. Some examples of apparent cell-roofing may

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possibly be due to diagenesis at the infilling-matrix surface, but some are the horizontal continuation of the lateral cell-walls, as seen in vertical section. In transverse section the cells are uniformly rounded-hexagonal, giving a honeycomb appearance. Oblique sections through the walls show no trace of intercommunicatory pores.

Some specimens show single examples of larger cells occurring among the normal cells. They are rounded-lenticular in outline, and are about three times the diameter of the ordinary cells of the particular growth in which they occur. In height they are the same or up to one and a half times that of the ordinary cells (Fig. 8). All these special cells are clearly roofed, unlike many of the other cells.

Trivial name. Commemorates Cartimandua, first-century Romano-British Queen of the Brigantes, from whose former territories the fossil comes.

Material. *Types.* British Museum (Natural History), Dept of Palaeontology, registered numbers V.21205d (Holotype: Fig. 7); V.21205b, V.21205c, V.21205d (Paratypes: Figs 2, 1, 3). From the Great Scar Limestone (Lower Carboniferous, Viséan D_1) of Mealbank Quarry, Ingleton, North Yorkshire, England.

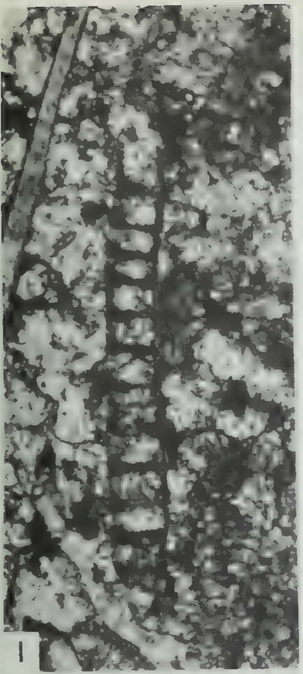
Other material. Numerous examples in eight further thin sections from the same sample, V.21205 (H. P. Lewis Coll., 1930). Also examples in four thin sections of the Oxford Limestone (Viséan D_2) of Dunsall Old Quarry, Berwick on Tweed, Northumberland, V.54331 (E. J. Garwood Coll.).

Discussion. This little organism occurs free and often apparently incomplete amongst the foraminifera, etc. of the parent rock. None have been seen clearly attached to solid objects; one doubtful example is probably an accidental juxtaposition. Nevertheless, the morphology suggests attachment, possibly to non-calcified algae, fixed or floating, presumably in shallow water. The North Yorkshire rock sample comes from a limestone quarry which shows evidence of emergence in a thin coal-seam with underclay (Kendal & Wroot 1924 : (I) 59; Hudson & King 1933 : 434), and the areal stratigraphy (Hudson 1933 : 247) indicates shallow marine conditions compatible with the habitat suggested. The Northumberland limestone does not conflict with this: it is similarly rich in foraminifera and microproblematica.

An animal origin, e.g. some lowly-organized colonial growth such as a simple extinct hydrozoan, seems unlikely in view of the very small cells and the absence of intercommunicatory pores through the walls. If, however, the cells are regarded as originally open on the upper or outer surfaces, the occasional closed examples being ascribed to either diagenesis or original abnormality, then this could support animal origin of some kind, with a tentative reproductive function for the special cells. There is a superficial resemblance and approximate size-correspondence to the Precambrian *Papillomembrana* (Spjeldnaes 1963, 1967), but this problematicum was probably carbonaceous not calcareous, cylindrical not plate-like, and the fringing projections are papillae, not wall-sections of polygonal mesh. If, however, *Hypocaustella* is considered as a small calcareous alga, size and lack of pores are in keeping, though there is still some uncertainty.

Monostromatic crusting corallines (Rhodophyta; family Corallinaceae) referable to the genus *Lithoporella* Foslie are common at the present day and in the Cenozoic (Lemoine 1974, 1976), usually attached to solid objects, organic or inorganic. The high-rectangular cells are squarish in

Figs 1–7 *Hypocaustella cartimanduae* gen. et sp. nov. Lower Carboniferous, Great Scar Limestone (Viséan D_1); Mealbank Quarry, Ingleton, North Yorkshire. Thin sections, × 120. V-numbers are registered numbers, Dept of Palaeontology, British Museum (Natural History). Fig. 1, rectangular cells, some roofed, in vertical cut; V.21205c. Fig. 2, small-celled individual showing branching; V.21205b. Fig. 3, polygonal cells in transverse cut; V.21205d (same thin section as holotype). Fig. 4, part of large-celled individual in vertical cut; V.21205e. Fig. 5, polygonal cells, slightly oblique view of walls in the thickness of the preparation; V.21205a. Fig. 6, special cell in centre of ordinary cells; V.21205f. Fig. 7, **holotype**. Apparently complete individual showing ordinary cells (left and right), special cell (top centre); twisting plane of organism gives polygonal view of cells (top left); V.21205d.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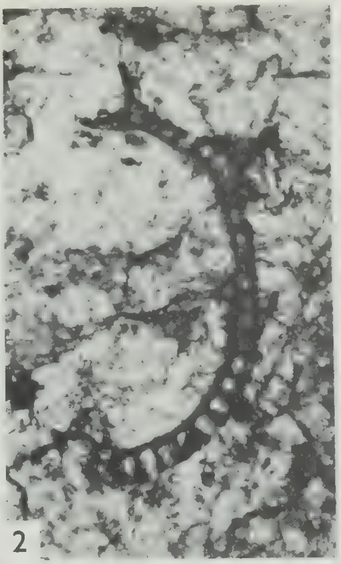
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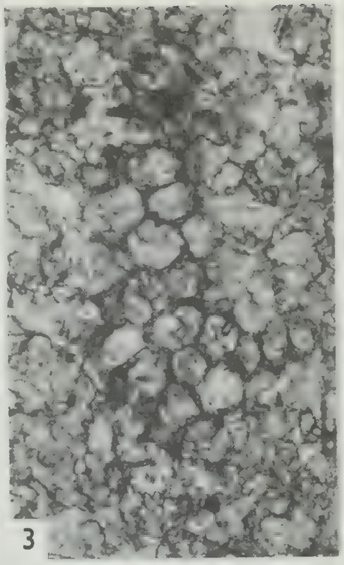
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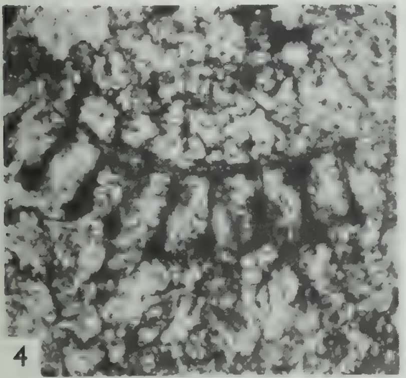
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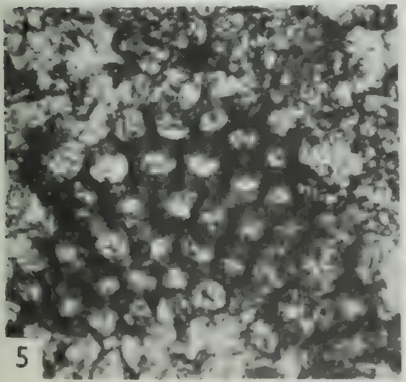
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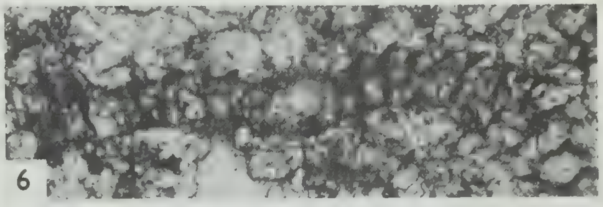
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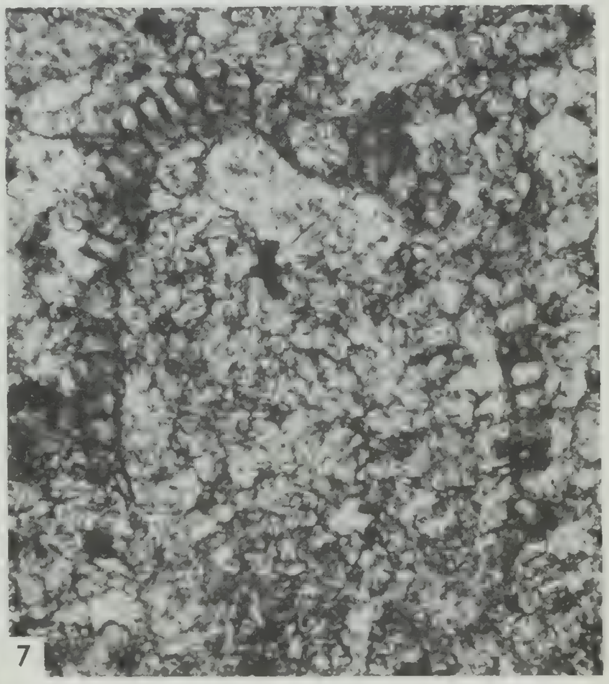
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transverse section; the conceptacles are large blister-like objects rising above the thin thallus. Calcification of the box-like cells is usually complete in the fossils.

In the Mesozoic, *Thaumatoporella* Pia (Trias–Cretaceous: syn. *Polygonella* Elliott, *Lithoporella* spp.) shows high-rectangular cells which are polygonal in cross-section: the calcification is sometimes incomplete, especially that of the upper cell-surfaces, but in numerous examples examined by me this appears to be due to the varying preservation. The conceptacles are rarely found, but are similar to those of *Lithoporella* (Emberger 1958). Like *Lithoporella*, *Thaumatoporella* seems to have been attached to solid objects.

Example	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Cell-height	30	30	36	40	40	45	45	45	54	54	63	63	72	80	80	108
Cell-width	20	30	36	20	40	30	36	45	36	40	36	36	45	40	45	54
Conceptacle-height	45			45							63	63				
Conceptacle-width	63			63							80	100				

Fig. 8 Tables of cell-dimensions (μm) in different examples of *Hypocaustella*.

Hypocaustella, then, is possibly to be regarded as a Palaeozoic algal growth of similar coralline nature from its vegetative thallus, the frequent absence of calcification on the upper or outer cell surfaces being due to non-preservation of an original thin calcification, and the attachment-habit being to non-calcified algae. If the larger cells are interpreted as conceptacles, they are clearly different from the very conspicuous structures seen in *Lithoporella* and *Thaumatoporella*. Can *Hypocaustella* be regarded as an ancestral monostromatic coralline alga?

Of other possible Palaeozoic claimants for this, the Permian *Archaeolithoporella* (Endo 1959 : 182) was accepted as such until recently. However, Babcock (1974 : 38) has shown that, although probably but not certainly algal, it is laminar but not cellular, and certainly not coralline; the significance of this is emphasized by Wray (1977). The peculiar *Litostroma oklahomense* (Pennsylvanian: Mamay 1959), whilst a monostromatic alga, possibly a rhodophyte, does not show conceptacles and does not seem to be a coralline. European records of this species, given in structural detail and reviewed by Homann (1972 : 170), who includes *L. europaea* Kochansky-Devidé (1970) as a synonym, yield no real evidence to make its taxonomic position more precise. *Stenophycus* (Devonian: Fenton 1943; Wray 1967) is a composite, doubtfully 'primitive coralline' structure which does show blister-like conceptacles but is not technically monostromatic. *Eolithoporella dawsoni* Johnson (1966), from the Canadian Mississippian, is perhaps the nearest to *Lithoporella*, but is based on very limited material and conceptacles are not known.

All of these have considerably larger thalli than *Hypocaustella*, and although of Upper Palaeozoic age, are very clearly spreads of roofed cells or laminae, with only occasional loss in preservation. *Hypocaustella* is curiously distinctive in this character, so its algal nature cannot be regarded as certain.

Pre-Cretaceous genera referred, often doubtfully, to the Corallinaceae are a scattered assemblage whose individual members seem to have become extinct. *Archaeolithophyllum* (not monostromatic: Johnson 1956) is the most convincing. If *Hypocaustella* is referable to this group, and this is not certain, it must be regarded as similarly individual, and not in the main evolutionary stream, since its 'conceptacles' are not of the characteristic large blister-like pattern. It would be unwise at present to extrapolate further from this isolated little organism, whose systematic position is so doubtful.

Acknowledgements

I thank Mr P. V. York, of the BM(NH) Photographic unit, for coping with the photography of these obscure little organisms: also Mr M. Crawley for preparing the table, Fig. 8.

References

Babcock, J. A. (1974). *The rôle of algae in the formation of the Capitan Limestone (Permian, Guadalupian), Guadalupe Mountains, West Texas–New Mexico.* 241 pp. Acad. Thesis, Univ. Wisconsin.

Emberger, J. 1958. *Lithoporella elliotti* nov. sp., mélobésiée nouvelle du Jurassique supérieur des Monts des Oulad-Nail, Atlas Saharien (Algérie). *Bull. Soc. géol. Fr.*, Paris, (6) **7** : 625–629.

Endo, R. 1959. Stratigraphical and paleontological studies of the later Paleozoic calcareous algae in Japan, XIV. Fossil algae from the Nyugawa Valley in the Hida Massif. *Sci. Rep. Saitama Univ.*, Urama, (B) **3** : 177–207.

Fenton, C. L. 1943. A new Devonian alga from Western Australia. *Am. Midl. Nat.*, Notre Dame, Ind., **30** : 112.

Homann, W. 1972. Unter- und tief-mittelpermische Kalkalgen aus den Rattendorfer Schichten, dem Trogkofel-Kalk und dem Tressdorfer Kalk der Karnischen Alpen (Österreich). *Senckenberg. leth.*, Frankfurt a.M., **53** : 135–313.

Hudson, R. G. S. 1933. The scenery and geology of north-west Yorkshire. *Proc. Geol. Ass.*, London, **44** : 228–255.

—— **& King, W. B. R.** 1933. The Yorkshire Dales: the Summer Field Meeting, 1933. *Proc. Geol. Ass.*, London, **44** : 428–440.

Johnson, J. H. 1956. *Archaeolithophyllum*, a new genus of Paleozoic coralline algae. *J. Paleont.*, Menasha, **30** : 53–55.

—— 1966. New Mississippian algae from Alberta. *J. Paleont.*, Menasha, **40** : 1385–1387.

Kendal, P. F. & Wroot, H. E. 1924. *Geology of Yorkshire. An illustration of the evolution of northern England.* xxii+995 pp., 2 vols. Leeds (privately published).

Kochansky-Devidé, V. 1970. Die Kalkalgen des Karbons vom Velebit-Gebirge (Moskovien und Kassimovien). *Palaeont. jugosl.*, Zagreb, **10.** 32 pp.

Lemoine, M. 1974. Contribution à l'étude du genre *Lithoporella* (Corallinacées). *Revue algol.*, **Paris, 11** : 42–57.

—— 1976. Le genre *Lithoporella* Foslie (algue Rhodophycée Corallinacée) au Tertiare et au Quaternaire. *Bull. Soc. géol. Fr.*, Paris, (7) **18** : 773–787.

Mamay, S. H. 1959. *Litostroma*, a new genus of problematical algae from the Pennsylvanian of Oklahoma. *Am. J. Bot.*, Lancaster, Pa., **46** : 283–292.

Spjeldnaes, N. 1963. A new fossil (*Papillomembrana* sp.) from the Upper Precambrian of Norway. *Nature, Lond.* **200** : 63–64.

—— 1967. Fossils from pebbles in the Biskopåsen Formation in southern Norway. *Norg. geol. Unders.*, Oslo, **251** : 53–82.

Wray, J. L. 1967. Upper Devonian calcareous algae from the Canning Basin, Western Australia. *Prof. Contr. Colorado Sch. Mines*, Golden, **3.** 76 pp.

—— 1977. Late Paleozoic calcareous red algae. *In* Flügel, E. (ed.), *Fossil algae: recent results and developments* : 167–176. Berlin, Heidelberg and New York.

Acanthopleurella Groom 1902: origin and life-habits of a miniature trilobite

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Synopsis

The Tremadoc genus *Acanthopleurella* includes the smallest of mature trilobites. The type species, *A. grindrodi*, is revised and a new species *A. stipulae* described. They both have four thoracic segments and were derived neotenously from a shumardiid ancestor by suppression of the release of two (?) segments. They were specialized, secondarily blind, burrowing deposit feeders. The extremely small size of *A. stipulae* enabled it to co-exist with *Conophrys salopiensis*, inhabiting the same substrate.

Introduction

In 1902 Professor Theodore Groom described the tiny trilobite *Acanthopleurella grindrodi* from the Tremadoc rocks of the Malvern Hills, but his material consisted only of internal moulds in an unsatisfactory state of preservation. Despite observations by Stubblefield (1926) and Lake (1946), and a figure by Bulman & Rushton (1973), the genus has remained little known. We have now, however, studied several good complete specimens, and not only confirm that *Acanthopleurella* is a valid genus with at least two species, but consider that it includes the smallest known adult trilobites. Its morphology is quite complex and it is possible to draw some functional conclusions concerning its mode of life and to investigate the possible causes of miniaturism in trilobites, a topic briefly considered by Robison & Campbell (1974).

In the form of its cranidium and glabella, the structure of the thoracic pleurae and the pygidium, *Acanthopleurella* is clearly related to *Shumardia* Billings, and in the discussion below we make many comparisons with the Shineton Shales species *Conophrys salopiensis* Callaway, a species formerly often referred to as *Shumardia pusilla* (Sars); this is not the place to discuss the validity of *Conophrys salopiensis*, but in using Callaway's name we intend to refer primarily to the well-known Shineton Shales form.

Miniaturized trilobites

Size. Although tiny, *Acanthopleurella* is not based on the young stages of larger trilobites. The only similar-looking forms are shumardiids, but Stubblefield (1926) showed that the form named *A. stipulae* here could not be regarded as normal growth-stages of *C. salopiensis*. Furthermore, the known size range of holaspids of *A. stipulae* (with four free thoracic segments) is considerable, from 1·07 mm to 1·50 mm. This indicates a greater size range than in any of the meraspid degrees of *C. salopiensis* described by Stubblefield (1926).

With a sagittal length of 1·07 mm to 1·50 mm *A. stipulae* appears to be the smallest trilobite known. Agnostids generally enter the holaspid condition at a length of 3 mm or more; the eodiscid *Opsidiscus* is 2 mm or more in length (cf. Westergård 1946). A small complete *Schmalenseeia* is 2·75 mm long (Westergård 1922 : pl. 1, fig. 19). The holotype of *Hospes clonograpti* Stubblefield (*in* Stubblefield & Bulman 1927 : 129) is 2·51 mm long; smaller specimens seem not

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to be holaspides. *Thoracocare minutum* Robison & Campbell (1974 : 278) reaches the holaspid state at a length of 1·7 mm and is in the meraspid condition at 1·15 mm (1974 : fig. 1B). Shumardiids are generally considerably larger, but Stubblefield recorded a *C. salopiensis* 'meraspis of degree 6' – a holaspis in more general if less precise terms – only 1·81 mm long; and *Shumardia nericiensis* Wiman (1905) is only about 2 mm long.

Origin. *Shumardia* and *Conophrys* are in any case small and most species have six thoracic segments (but some species have five or seven). *Acanthopleurella* has only four, and part of the miniaturization of the genus is produced by reduction of the number of segments. But it is not as simple as that. *Acanthopleurella* holaspides with four segments are larger than degree 4 meraspides of *Conophrys salopiensis* (Fig. 12). Stubblefield has shown that in *Conophrys* the fourth, macropleural, segment, after being released from the transitory pygidium, migrates forwards in successive moults as the posterior two segments are added. In *Acanthopleurella* the process stops after the release of the fourth segment, which is presumed to be homologous with the macropleural fourth segment in *Conophrys*. The third thoracic segment on *Acanthopleurella* is also spinose, and on the meraspis *three* pairs of spines are present (Fig. 19). Hence during its ontogeny segments bearing the first two spines migrate forwards to be released as the two segments with spinose pleurae, while the posterior, third pair is aborted.

It is reasonable to assume that the *Conophrys* condition, generally with six segments, is primitive, and the *Acanthopleurella* condition, with four, is derived. The six-segment condition is also persistent, since the much younger species *Shumardia granulosa* Billings (redescribed in Whittington 1965) also has six segments. There may have been a five-segment stage between a *Conophrys*-like ancestor and *Acanthopleurella* (*C. ?curta* Stubblefield has five segments), but since there are

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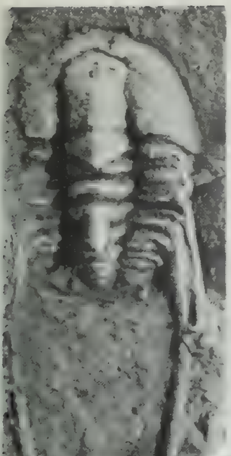
Figs 1–4 *Acanthopleurella grindrodi* Groom. All ×20. Fig. 1, IGS TW454A. Latex cast of dorsal exoskeleton. Figd Bulman & Rushton (1973 : pl. 6, fig. 6). Combe Abbey no. 1 Borehole, near Coventry, at 76 m depth. Fig. 2, IGS Zg184. Latex cast of dorsal exoskeleton. Bronsil Shales, south of Chase End Hill, near Malvern. Fig. 3, Holotype, University Museum, Oxford, A7. '*Dictyonema*-shales' of the Malvern Hills. Imperfectly preserved internal mould, partly enrolled. Mould of the macropleural spine on the left appears as dark hole. Figd Groom (1902 : fig. 3) and Lake (1907 : pl. 4, fig. 3). Fig. 4, Paratype, University Museum, Oxford, A8. Internal mould of thorax and pygidium, loc. as for Fig. 3. Figd Groom (1902 : fig. 4).

Figs 5–10, 13–15, 19 *Acanthopleurella stipulae* sp. nov. All ×20 except Fig. 19. Shineton Shales, Sheinton Brook, loc. 'RR2' of Stubblefield & Bulman (1927 : pl. 5). Fig. 5, Latex cast of **holotype**, complete exoskeleton, with associated cranidium. IGS Zs6184. Note genal spines. Fig. 6, IGS Zs6186, cranidium showing anterolateral lobes. Fig. 7, IGS GSM 58712, smallest holaspis, figd Lake (1907 : pl. 4, fig. 4). Fig. 8, BM(NH) In26816a, holapsis with damaged axis and pyritized spines. Figd Stubblefield (1926 : pl. 15, fig. 16). Fig. 9, IGS Zs6187, pygidium, poorly preserved internal mould but with pyritized border showing granules. Fig. 10, IGS Zs6182, pygidium showing large tubercles on pleural fields and well-developed anterior segment. Fig. 13, IGS Zs6185, meraspid of degree 3, showing pygidial doublure and pyritized spines on third thoracic segment and anterior of transitory pygidium. Fig. 14, IGS GSM 48713, largest holaspis, figd Lake (1907 : pl. 4, fig. 2). Fig. 15, Latex cast of BM(NH) In 26816b, showing large articulating half-ring on third thoracic segment. Fig. 19, Scanning electron micrograph of latex cast from meraspis of degree 0 on same rock chip as holotype. Note marginal spines and suture between cephalon and protopygidium. ×90.

Figs 11–12, 16–17 *Conophrys salopiensis* Callaway. Shineton Shales, Sheinton Brook, loc. 'RR2' of Stubblefield & Bulman (1927 : pl. 5). Fig. 11, BM(NH) In26819, ×9, internal mould of complete exoskeleton in oblique side view to show facial suture. Figd Stubblefield (1926 : pl. 16, fig. 20). Fig. 12, BM(NH) In26815, ×20, internal mould of meraspis degree 4 showing macropleural spine on fourth segment. Figd Stubblefield (1926 : pl. 15, fig. 15). Figs 16, 17, IGS Zs6188 (Stubblefield & Bulman coll.), latex cast of exceptionally well preserved complete exoskeleton, dorsal and oblique lateral views, ×9, showing facial suture and free cheeks, possibly conjoined.

Fig. 18 *Conophrys* sp. IGS RU5885. Entire exoskeleton showing seven thoracic segments, ×15. Lower Tremadoc Series, tributary of Nant-y-Gist-faen, near Arennig Fawr, North Wales.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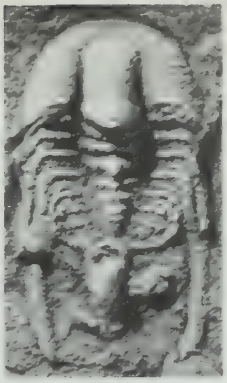
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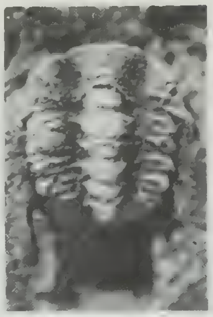
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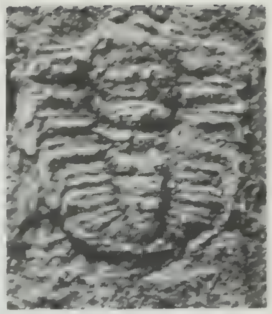
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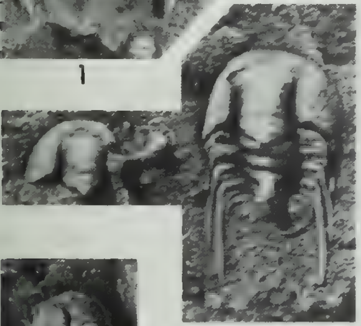
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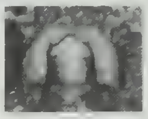
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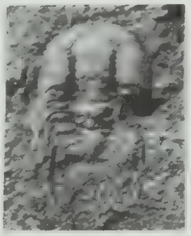
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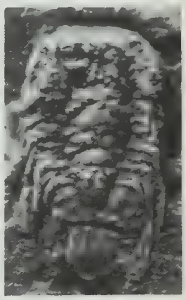
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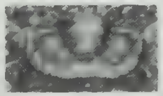
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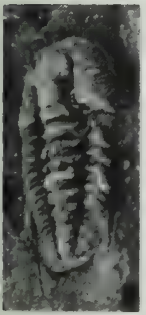
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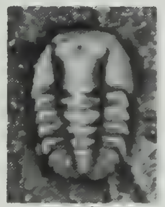
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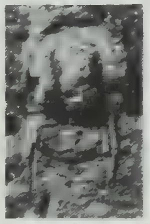
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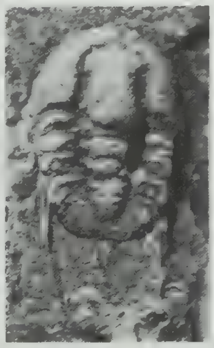
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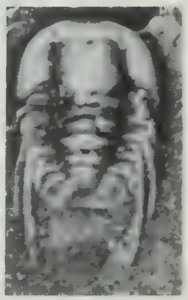
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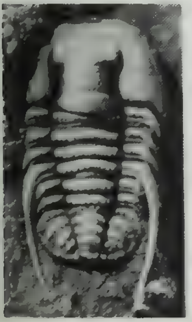
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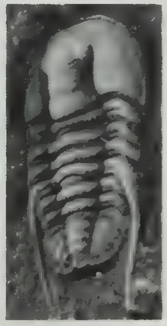
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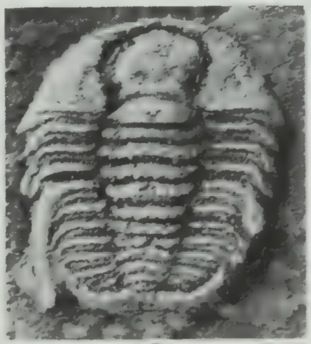
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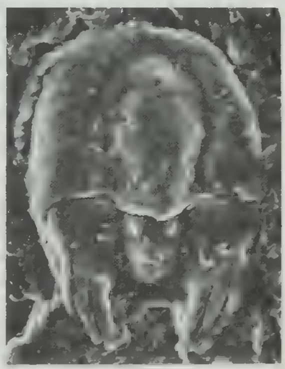
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examples (e.g. *Ceraurinella*, see Whittington & Evitt 1954) where several thoracic segments are released simultaneously into the thorax from the transitory pygidium, it seems perfectly possible to us that elimination of the release of two segments may have occurred as a single evolutionary step. Since *Acanthopleurella* had to be sexually mature, even at this small size, what essentially happened was a movement backwards (ontogenetically speaking) of sexual maturity – the process usually known as paedomorphosis.

A possibility that has to be reviewed is that *Acanthopleurella* was a sexual dimorph of *Conophrys*. This is improbable. In the first place the two forms are not invariably found together. For example, in the Amnodd Shales (near Arennig Fawr, Gwynedd) *Conophrys salopiensis* is common, but no example of *Acanthopleurella* has been discovered. Conversely at Malvern we have not noted a *Conophrys* from the same beds as *Acanthopleurella grindrodi*. If of opposite sex they would evidently have encountered one another very rarely! One might also expect, generally, *Shumardia*-like species would in that event tend to come in 'pairs', one male and one female morph occurring together. In our experience this is not so. In the early Ordovician of Spitsbergen, for example, where three species of shumardiid occur, they are found in sequence rather than together. Similarly the Shumardia Limestone in Quebec seems to contain only a single species, and that in great abundance.

Life habits

The present example of miniaturization is not unique. Robison & Campbell (1974) have described a Cambrian corynexochoid trilobite *Thoracocare* with only two thoracic segments in the holaspid stage. It is likely that a similar process of miniaturization was involved in the genesis of the Agnostacea. Jell (1975) has discussed polymorphism in *Pagetia*, in which two- or three-segmented forms are recognized within a single species.

Robison (1972) and Jell (1975) concur that trilobites of the Agnostida (*sensu* Salter 1864) were pelagic or planktonic in habit. The same habits were deduced for *Thoracocare* (Robison & Campbell 1974). It should be noted, however, that some authors have proposed different life habits for the agnostids: for example, Bergström (1973) has suggested that they may have been parasitic on some (unspecified) free-swimming organism whereas Pek (1977) has presented evidence that some forms may have been epipelagic upon some floating seaweed, and Jago (1973) has suggested that they show some community behaviour related to former sea-bottom conditions, and hence may have included some benthic forms.

Thoracocare has large eyes and a very large pygidium, and is not really comparable to *Acanthopleurella* in its morphology. Agnostids were blind, like *Acanthopleurella*, but beyond this and their small size morphological comparisons cannot be extended in detail. Powerfully spinose agnostids are unusual, and we can only find one species in which the pleurae are spinose in the manner of *Acanthopleurella* (*Lejopyge laevigata armata* Westergård, 1946 : pl. 13, figs 32–36).

At the small adult size of *Acanthopleurella* genal and thoracic spines would have been effective in increasing frictional drag during descent through the water column. Many protaspides, which were supposedly planktonic, are well equipped with spines which would have inhibited sinking, as are Recent crustacean larvae. However, in this case we do *not* believe that the spines functioned as frictional brakes. In the first place they lie more or less horizontally alongside the thorax, so that in dorsal view they are not disposed in a way which would have been particularly effective in inhibiting sinking. If this had been their principal purpose one would have expected them to have been splayed out in the manner of odontopleurids, such as *Miraspis*, to present as large a surface area as possible. Second, the mid-thoracic spine would have had no influence on frictional drag. Third, *Acanthopleurella* seems to have had a very restricted distribution, being confined to Tremadoc shales of the Welsh borderlands and the English Midlands, not even extending over the whole region from which *Conophrys salopiensis* has been recovered. Fortey (1974 : fig. 4) has shown that pelagic trilobites tend to have an exceptionally elongate exoskeleton, whereas *Acanthopleurella*, the transverse width of which at mid-thorax is about three-quarters the length (sag.), is not unusual in this regard. The balance of the evidence suggests that *Acanthopleurella* was benthic, and the fact that the meraspis degree 0 already had assumed the morphology characteristic of the adult further suggests that this habit was acquired from an early stage in ontogeny.

Some specimens (Figs 8, 15) show well-developed articulating half-rings, extending to almost the entire length of the preceding thoracic axial ring on the segments anterior to the macropleural segments. This implies considerable longitudinal flexibility. Given this fact, the lack of pleural spines on the first two thoracic segments can be explained: had spines been present on the first two segments any downward flexure of the cephalon (resulting in an upward swing of the genal spines) would have been prevented. Fig. 5 shows well how closely the genal spines approach the third thoracic segment.

Assuming benthic habits, we can extend the analysis of functional aspects of *Acanthopleurella* to enrollment. It is extremely unlikely that enrollment would have occurred by movement of the thorax relative to the cephalon, as this would have involved dragging the relatively enormous thoracic spines through the sediment. On the other hand, enrollment could have been achieved relatively easily by tucking the cephalon down and backwards beneath the pygidium; the short anterior thoracic pleurae permit unimpeded downward flexure of the cephalon. Most of the flexure seems to have been accommodated at the forward margin of the first, second and third segments, where, as we have noted, remarkably broad (sag.) articulating half-rings are developed. The resulting enrolled position might well have utilized the long backward-directed spines on the third and fourth thoracic segment as a means of support on the sediment surface during enrollment.

Both *Conophrys* and *Acanthopleurella* lack eyes, and, as in all trilobites, the blindness was secondary, as shown by the librigenal remnants figured in Figs 20a, b. We can eliminate great oceanic depth (Clarkson 1967) as a possible cause for this blindness because almost all the trilobites found in association with these shumardiids had normal eyes (except the agnostids), and were not different in eye development from other 'shelf' assemblages of the Tremadoc.

Blindness is explained by inferring that *Acanthopleurella* burrowed superficially in the surface layer of the argillaceous sediments with which it is associated, a life mode which rendered eyes superfluous. Reasonable support for this hypothesis is derived from a consideration of extant infaunal, minute crustacea. Even at 1–2 mm long *Acanthopleurella* is too large to be considered as a possible interstitial (meiofaunal) inhabitant, like the Mystacocarida, although visual surfaces are generally reduced in those forms. The best, and rather close, analogy is perhaps with cephalocarids (Sanders 1963). *Hutchinsoniella macracantha* has an adult length of 3 mm (excluding caudal spines) with a broadly hemispherical cephalon. It is blind, but secondarily so. It is benthic from early in its ontogeny, which, like that of shumardiids (but not of all trilobites), is a simple, progressive addition of segments without any profound morphological change. The principal morphological difference is the vermiform and flexible posterior segments of *Hutchinsoniella*. As we have inferred for *Acanthopleurella*, *Hutchinsoniella* lives in soft, muddy sediments. *Hutchinsoniella* extracts edible particles from detritus by using its limbs as a kind of filtration device. Whether or not *Acanthopleurella* used its limbs in the same way, it seems reasonable to suppose that it also extracted organic particles from the sediment. It is also worth noting that shumardiids occur in association with ostracods, with valve dimensions similar to the transverse cephalic dimensions of *Acanthopleurella* and *Conophrys* (Stubblefield & Bulman 1927; Bulman & Rushton 1973 : pl. 6). Benthic ostracods are also frequently deposit feeders, and it is not unreasonable to suppose that these arthropods were also concerned with exploiting the same source.

The occipital ring of *Acanthopleurella stipulae* is long (sag.) and produced backwards. This feature acquires significance if we assume that *Acanthopleurella* adopted an active feeding position with the cephalon tilted through an angle of perhaps 20° (Fig. 21c), in a manner similar to that shown by Clarkson (1969) for the Silurian odontopleurid *Leonaspis deflexa*. In this attitude the prolonged occipital ring serves to cover the 'gap' which would otherwise be created between thorax and cephalon. The genal spines then tilt upwards past the first two thoracic segments. Note that in *Leonaspis deflexa* the anterior thoracic pleural spines are (for an odontopleurid) also relatively abbreviated.

As a final comment on the function of the macropleural spines Ingham (1968 : fig. 3) has suggested that in *Cybeloides girvanensis*, a species equipped with long macropleurae, the spines

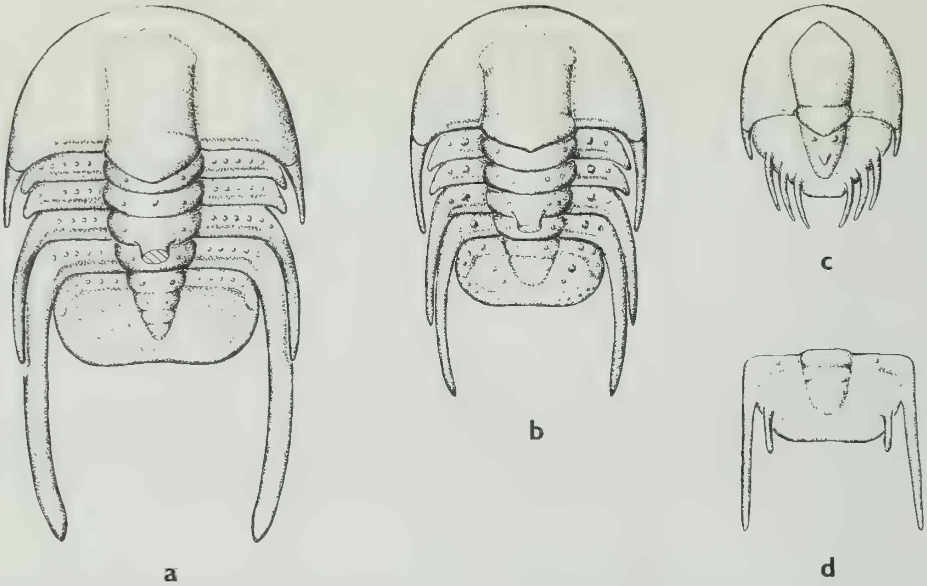

Fig. 20 (a) Reconstruction of *Acanthopleurella grindrodi* Groom, × 30. (b–d) *A. stipulae* sp. nov.; (b) reconstruction, × 30; (c) meraspid of degree 0, × 60, reconstructed from Fig. 19; (d) pygidium of meraspid degree 3, × 60, based on an internal mould on the same rock-chip as the holotype.

functioned as an aid in burial, and that the long macropleural spine had a stabilizing function 'preventing excessive lateral rolling during arching of the thorax' while burial was in progress. *Acanthopleurella* may have spent a large part of its life buried at least within the semi-fluid surface layer of sediment. The vertical spine from the middle of the third thoracic segment, which we have not so far discussed, seems ideally placed to have acted as a sensor to make sure that burial did not proceed too far. At the minute size of *Acanthopleurella* we do not consider that the spines would have had a particular defensive function.

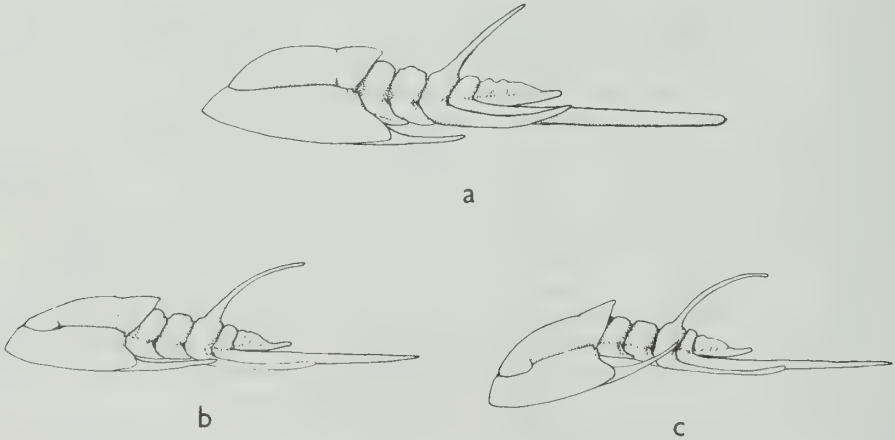

Fig. 21 (a) Lateral view of *Acanthopleurella grindrodi*, × 30; (b), (c) lateral view of *A. stipulae*, × 30, in relaxed attitude (b) and in 'active' feeding or grubbing attitude (c). Length of dorsal axial spines and anterior course of facial sutures conjectural.

Summary of life habits. *Acanthopleurella* was derived from a *Conophrys*-like ancestor by suppression of release of two segments during ontogeny. It was a blind, benthic animal, but did not inhabit a particularly deep water environment. It was probably a burrowing deposit feeder, using its long macropleural spines as a support at or just below the sediment surface, during enrollment, and as an aid to burial.

Resource partitioning and the relation of *Conophrys* to *Acanthopleurella*

Robison (1975) was the first to examine the effect of competitive exclusion in controlling the numbers of species and adult size of sympatric agnostids. Where related sympatric species utilize the same resource they can coexist without mutually exclusive competition if they exploit the resource in different ways, for example by taking different particle sizes if they are deposit feeders. May (1973) has given the mathematical basis for this kind of resource partitioning. Applications of this theory to marine benthos living on soft bottoms are relatively limited, but it has been applied to the small (*c.* 3 mm) benthic gastropod *Hydrobia* by Fenchel (1975). This is an appropriate example in the present case because *Hydrobia* is a small deposit feeder, and may exploit a resource and particle size not so very different from that utilized by shumardiids. Differences in particle-size utilization are reflected more or less directly in differences in adult size of the exploiting animal. Robison (1975) showed that the ratio between lengths of 'neighbouring' agnostids commonly approached the theoretically predicted value of 1·3 (and up to about 1·5). We do not have anything like the number of specimens of *Acanthopleurella* that Robison used for his agnostid example, but we can compare the length (sag.) of largest *A. stipulae* with average holaspid length of *Conophrys salopiensis* obtained from Stubblefield (1926). The length ratio of the latter to the former is about 2·2, which indicates that the size-difference between the two forms was more than adequate to allow them to exploit the same resource without direct competition. This ratio is far larger than the theoretical minimum. There is another small blind trilobite in the British Tremadoc, *Hospes clonograpti* Stubblefield (*in* Stubblefield & Bulman, 1927) which almost exactly serves to bridge the size gap: the length ratio of *Hospes* to *Acanthopleurella* is about 1·7, and that of *Conophrys* to *Hospes* is about 1·3. It is possible that *Hospes*, too, exploited the same environment. However, it has not so far been found in the beds that have yielded *Acanthopleurella* and *Conophrys*.

The shumardiid example is particularly interesting because we know the mechanism by which the morphological difference necessary to avoid competition was achieved, in this case the shortening of the thorax. There are other families of trilobites in which the number of thoracic segments is highly variable, for example the Olenidae, and similar adaptive reasons may prove to be behind otherwise inexplicable differences in thoracic development.

Systematic descriptions

Family **SHUMARDIIDAE** Lake, 1907

Genus *ACANTHOPLEURELLA* Groom, 1902

TYPE SPECIES. *Acanthopleurella grindrodi* Groom, 1902, by monotypy.

DIAGNOSIS. Minute, blind, opisthoparian shumardiid trilobites. Glabella without lateral furrows, but faint anterolateral lobes may be developed. Occipital ring long sagittally but not spined. Genal spines present on free cheeks. Thorax of four segments, the third bearing an axial spine, the third and fourth having long pleural spines. Pygidium transverse, with border, pleural fields flat; anterior segment well defined, segmentation obscure posteriorly.

REMARKS. *Acanthopleurella* differs from *Conophrys* most obviously in the shorter thorax and the presence of macropleural spines on the third as well as the fourth segment. *Conophrys salopiensis* Callaway (=*Shumardia pusilla* auctt.), from the Shineton Shales, has six thoracic segments of which the fourth only has macropleural spines. Other *Conophrys* may have seven segments (e.g. *C.* sp. of Bulman & Rushton (1973 : pl. 6, fig. 5) and another undescribed species (Fig. 18) from the lowest Tremadoc of North Wales) but in these only the fourth segment is macropleural. *C.? curta* Stubblefield has five thoracic segments and again only the fourth is macropleural. No *Conophrys* are known to have thoracic axial spines.

The cephalon of *Acanthopleurella* is less distinctive: the anterolateral lobes are weaker than in *C. salopiensis* but are not weaker than those of *C.? curta* or the *C.* sp. of Bulman & Rushton, or the cranidia referred to *Shumardia alata* Robison & Pantoja-Alor (1968 : 797). Whittington (1965 : 329) showed that *S. granulosa* has free cheeks and suggested that the Shineton Shales '*S. pusilla*' might also have them, although the evidence he cited, Lake's pl. 4, fig. 1, is based on a figure of a young *Asaphellus* (Lake 1942 : 324). Nevertheless, we find that Whittington's suggestion is supported by Shineton Shales specimens (Figs 11, 16, 17). Unlike *Acanthopleurella*, *C. salopiensis* does not show genal spines, although a possible *Conophrys* species, '*Shumardia*' *oelandica* Moberg (1900 : pl. 14, fig. 4a), is illustrated with apparently fixigenal spines, and '*S.*' *nericiensis* Wiman seems to have librigenal spines (Wiman 1905 : pl. 2, fig. 14).

The pygidia of *Conophrys* and *Shumardia* species vary greatly in shape and in the characters of the border and doublure. *Acanthopleurella* pygidia are short and wide with flat pleural fields and tend to be slightly emarginate behind the axis. In this they differ strongly from *S. granulosa* but resemble some *Conophrys*.

Acanthopleurella grindrodi Groom, 1902

Figs 1–4, 20a, 21a

1902 *Acanthopleurella grindrodi* Groom : 70, figs 1–4.
1907 *Shumardia pusilla* (Sars); Raw *in* Lake : 42 (*pars*); pl. 4, fig. 3 only [figures holotype and places it in synonymy of *S. pusilla*].
1946 *Acanthopleurella grindrodi* Groom; Lake : 341 [revives *Acanthopleurella*].
1973 *Acanthopleurella* sp.; Rushton *in* Bulman & Rushton : 25; pl. 6, fig. 6.

TYPE SPECIMENS. Holotype OUM A7 (Fig. 3), the original of Groom's (1902) fig. 3. Paratype OUM A8 (Fig. 4), the original of Groom's fig. 4. Both are from the '*Dictyonema*-shales of the Malvern Hills', from beds correlated by Stubblefield & Bulman (1927) with parts of the *Dictyonema flabelliforme* Zone or the Transition Beds of the Shineton Shales.

OTHER MATERIAL. IGS Zg183, Zg184, J. C. Harper coll. From Bronsil Shales (Tremadoc) south of Chase End Hill, Malvern Hills. IGS TW454A from Tremadoc shales in the Combe Abbey no. 1 Borehole, 6 km east of Coventry; the age of these beds is a matter of some doubt (Bulman & Rushton 1973 : 7–8, 11).

DIAGNOSIS. *Acanthopleurella* without distinct anterolateral glabellar lobes; occipital ring about one-third the width of cranidium; posterior macropleura relatively massive, nearly as long as sagittal length of trilobite. Pygidial axis with four segments, pointed behind; pleural fields of thorax and pygidium with rows of many but inconspicuous granules.

MEASUREMENTS. IGS Zg184: sagittal length = 1·70 mm, length of cephalon (maximized) = 0·92 mm, width of cranidium (estimated) = 1·42 mm, length of fourth segment = 1·5 mm, length of pygidium = 0·55 mm, width of pygidium = 1·01 mm. TW454A: sagittal length = 2·03 mm. The holotype has a pygidium 0·48 mm long and 0·92 mm wide; the paratype pygidium is 0·60 mm long and 1·25 mm wide.

REMARKS. The type specimens are rather poorly preserved and do not show several features taken here to be characteristic of *A. grindrodi* (cf. Rushton *in* Bulman & Rushton 1973 : 26). We interpret the species by reference to IGS Zg184 (Fig. 2) and do not see any significant primary differences between that specimen and Groom's types. The holotype does not show the macropleura on the third segment, probably because the shale has split at a level lower than that at which the spine was preserved, but the mould of the spine on the fourth segment is clear (Fig. 3). We see no evidence for the four pairs of macropleurae shown in Groom's (1902) fig. 1. Groom's interpretation of the cephalon is based on its posterior half only, the anterior part of the cephalon being folded under and not clearly visible.

A. grindrodi was described by Rushton (*in* Bulman & Rushton 1973) on the basis of one specimen which resembles Zg184 in almost all particulars (Fig. 1). Rushton's description should be amended because he described the cranidium as a cephalon. IGS Zg183 shows small free cheeks with a genal spine about half as long as the cranidium. The punctate surface doubtfully observed by Rushton cannot be confirmed by other specimens. In Zg184 the thoracic axis is a little wider than the occipital ring. Pairs of small granules are placed exsagittally on the pleural and pygidial axial rings, and rows of small granules are present on the anterior bands of all the thoracic and pygidial pleurae as well.

This species is contrasted with the new form *A. stipulae* below.

Acanthopleurella stipulae sp. nov.

Figs 5–10, 13–15, 19, 20b–d, 21b, c

1907 *Shumardia pusilla* (Sars); Raw *in* Lake : 42 (*pars*); pl. 4, figs 2, 4.
1926 *Shumardia pusilla* variety ?; Stubblefield : 257–258; pl. 15, fig. 16 [distinguished from *S. pusilla*].
1946 *Acanthopleurella*; Lake : 341 (*pars*) [revives *Acanthopleurella*].

HOLOTYPE. IGS Zs6183–4, counterparts (Fig. 5), Stubblefield & Bulman coll. Shineton Shales, *Shumardia pusilla* Zone, Sheinton Brook, south of Sheinton, Salop. Locality 'RR2' of Stubblefield & Bulman (1927 : map, pl. 5).

PARATYPES. BM(NH) In.26816, complete specimen; IGS Zs6181–2, 6185–7, 4 complete specimens (2 immature), 4 cranidia, 3 pygidia (1 immature), all Stubblefield & Bulman coll. IGS GSM 48712, 48713, Rhodes coll. All are from the same locality as the holotype.

DIAGNOSIS. *Acanthopleurella* with distinct anterolateral lobes; occipital ring wider than fixed cheeks; posterior macropleura about half sagittal length of trilobite; pygidial axis short and blunt; pleural regions of thorax and pygidium with few but conspicuous granules.

NAME. 'Of stubble', with reference to Sir James Stubblefield.

DESCRIPTION. Cranidium convex, length two-thirds of width. Cephalic axis four-fifths or more of cranidial length and two-fifths of its width. Glabella bluntly pointed in front, defined by distinct axial furrow; weak but distinct anterolateral lobes mark its widest part, behind which the sides of the glabella are slightly concave; no glabellar furrows. Occipital furrow weakly marked, nearly transverse. Occipital ring about as wide as widest part of glabella and nearly half as long, produced backwards in a broad curve, with a faint median node on its posterior edge. Fixed cheeks curved down frontally and laterally, without eyes or eye-ridges. Posteriorly the fixed cheek is two-thirds of the width of the occipital ring, abaxially curves somewhat backwards and downwards to the rounded posterolateral corner where the facial suture cuts off the genal spine. No border except posteriorly, where a short pleuroccipital furrow defines a narrow depressed border near the glabella, but dies out before reaching the facial suture. Facial suture appears to be nearly marginal for most of its course but cuts off the genal spines at the posterolateral corners. Genal spine depressed below the level of the first two thoracic pleurae but the tip curves up to clear the third pleura. Exoskeleton smooth.

Adult thorax of four segments. Axis of first two segments nearly twice as wide as pleura. Axis of third ring narrower and bears a large backwardly- and upwardly-directed spine of unknown length. The first and fourth axial rings bear pairs of small exsagittally-placed granules; the second and third axial rings have two pairs of such granules. First and second pleurae short, third and fourth pleurae have long spines, the macropleura on the fourth segment being over half the length of the rest of the trilobite. Stubblefield (1926 : 358) interpreted the specimen here refigured (Fig. 8) as having a spine on the second as well as the third and fourth pleurae. Our interpretation is that the genal spines have been displaced slightly backwards, perhaps during moulting, so that the spine has a somewhat anomalous position alongside the second and first segments. We believe that we can recognize the sutural margin on the spine that identifies its genal origin. The 'trace of a genal spine' also noted by Stubblefield cannot now be observed on the specimen. The pleurae each have two granules on the anterior pleural band, the granule nearer to the axial furrow being the larger and comparatively conspicuous.

Pygidium with length about half the width, outline posteriorly faintly emarginate. The axis occupies just over one-third of the greatest width, is shorter than wide and truncate behind; composed of one well-defined ring, one or possibly two fainter ones behind and a terminal piece; the anterior ring carries a pair of small exsagittally-placed granules. Pleural fields flat, composed of one well-defined segment with a trace of one or two more behind. Conspicuous granules on the pleural fields continue the exsagittal arc of conspicuous granules seen on the thoracic pleurae. Posterior border weakly defined, furnished with small granules (Fig. 9). Width of doublure about one-fifth of pygidial length.

MEASUREMENTS. Holotype: sagittal length of trilobite = 1·32 mm, length of cranidium (maximized) = 0·70 mm, width of cranidium (estimated) = 1·1 mm, length of fourth segment = 0·78 mm, length of pygidium = 0·32 mm, width of pygidium = 0·65 mm. Length of BM(NH) In.26816 is 1·40 mm if allowance is made for the crushed front of the cephalon. IGS GSM 48713 and 48712 are 1·50 mm and 1·07 mm long respectively.

REMARKS. *A stipulae* differs from *A. grindrodi* in its relatively wider axis. The glabella has more definite anterolateral lobes than in *A. grindrodi* and the occipital ring has a faint median node. In *A. stipulae* the pleural regions have fewer but larger granules than in *A. grindrodi* and the axes of the second and third segments have an extra pair of exsagittal granules. The macropleura on the fourth segment is not as massive as that of *A. grindrodi* but appears to have a sharper tip. The pygidial axis has a shorter, blunter axis with one or two fewer rings. The available material suggests that *A. stipulae* is a smaller species than *A. grindrodi*.

Stubblefield (1926 : 357–358) discussed the differences between the form named here as *A. stipulae* and meraspid specimens of *Conophrys salopiensis* ('*Shumardia pusilla*') with four thoracic segments (Fig. 12). The principal differences include the larger anterolateral glabellar lobes of *C. salopiensis*, its single macropleural segment and the stronger segmentation of the pygidium. We would emphasize also the large occipital ring and the axial spine on the thorax of *A. stipulae*. Meraspids of degree 4 reach 1·06 mm in length (Stubblefield 1926 : 356), and thus almost overlap the lower size-range of *A. stipulae* holaspides.

The presence of weak anterolateral lobes in *A. stipulae* recalls the condition of immature specimens of the associated shumardiid *C. salopiensis* (cf. Stubblefield 1926 : pl. 14, fig. 6; pl. 15, fig. 15). The only shumardiid known to be associated with *A. grindrodi* is the *Conophrys* sp. figured by Bulman & Rushton (1973 : pl. 6, fig. 5) which, like *A. grindrodi*, shows scarcely a trace of anterolateral lobes even though the specimen is apparently full-grown.

DEVELOPMENT. A meraspid of degree 0 is associated with the holotype of *A. stipulae*. It is 0·45 mm long and has a comparatively narrow axis. It has three pairs of spines which spring from the edge of the dorsal side of the transitory pygidium (Figs 19, 20c).

Also associated with these specimens is a transitory pygidium of a meraspid degree 3 (Fig. 20d). It is an internal mould with a sagittal length of about 0·22 mm, the 'true' pygidium being about 0·15 mm long. The long macropleural spine is that of the fourth thoracic segment, not yet released; behind this is a smaller macropleural segment (reconstructed here from the base of the spine on the internal mould and a trace of the external mould of the free spinose tip). It represents the third pair of spines seen in the meraspid of degree 0, partly reduced such that in the holaspid stage the pleural region of the pyridium is no longer spinose. The specimen shown in Fig. 13 is a complete meraspid, degree 3. The transitory pygidium has a sagittal length of 0·30 mm, the 'true' pygidium being about 0·22 mm long, and shows the bases of the reduced third pair of spines. It also shows the broad pygidial doublure. The smallest holaspis (Fig. 7) has a pygidium 0·25 mm long.

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References

Bergström, J. 1973. Organisation, life and systematics of trilobites. *Fossils Strata*, Oslo, **2** : 1–69, 5 pls.

Bulman, O. M. B. & Rushton, A. W. A. 1973. Tremadoc faunas from boreholes in Central England. *Bull. geol. Surv. Gt Br.*, London, **43** : 1–40, pls 1–7.

Clarkson, E. N. K. 1967. Environmental significance of eye-reduction in trilobites and Recent arthropods. *Mar. Geol.*, Amsterdam, **5** : 367–375.

—— 1969. A functional study of the Silurian odontopleurid trilobite *Leonaspis deflexa* (Lake). *Lethaia*, Oslo, **2** : 329–344.

Fenchel, T. M. 1975. Character displacement and coexistence in mud snails (Hydrobiidae). *Oecologia*, Berlin, **20** : 19–32.

Fortey, R. A. 1974. A new pelagic trilobite from the Ordovician of Spitsbergen, Ireland and Utah. *Palaeontology*, London, **17** : 111–124, pls 13, 14.

Groom, T. T. 1902. On a new trilobite from the *Dictyonema*-shales of the Malvern Hills. *Geol. Mag.*, London, (4) **9** : 70–73.

Ingham, J. K. 1968. British and Swedish species of *Cybeloides* (Trilobita). *Scot. J. Geol.*, Edinburgh, **4** : 300–316, pls 1, 2.

Jago, J. B. 1973. Cambrian agnostid communities in Tasmania. *Lethaia*, Oslo, **6** : 405–421.

Jell, P. A. 1975. Australian Middle Cambrian eodiscoids with a review of the superfamily. *Palaeontographica*, Stuttgart, (A) **150** : 1–97, 9 pls.

Lake, P. 1906–1946. British Cambrian trilobites. **2** (1907) : 29–48, pls 3, 4; **13** (1942) : 307–332, pls 44–46; **14** (1946) : 333–350, pl. 47. *Palaeontogr. Soc.* (*Monogr.*), London.

May, R. M. 1973. Stability and complexity in model Ecosystems. *Monogr. Popul. Biol.*, New Jersey, **6.** 265 pp.

Moberg, J. C. 1900. Nya bidrag till utredning af frågen om gränsen mellan undersilur och kambrium. *Geol. För. Stockh. Förh.* **22** : 523–540, pl. 14.

Pek, I. 1977. Agnostid trilobites of the Central Bohemian Ordovician. *Sb. geol. Věd. Praha*, P **19** : 7–44, 12 pls.

Robison, R. A. 1972. Mode of life of agnostid trilobites. *24th Int. Geol. Congr.*, Montreal, **7** (Palaeont.) : 33–40.

—— 1975. Species diversity among agnostoid trilobites. *Fossils Strata*, Oslo, **4** : 219–226.

—— **& Campbell, D. P.** 1974. A Cambrian corynexochoid trilobite with only two thoracic segments. *Lethaia*, Oslo, **7** : 273–282.

—— **& Pantoja-Alor, J.** 1968. Tremadocian trilobites from the Nochixtlán region, Oaxaca, Mexico. *J. Paleont.*, Tulsa, **42** : 767–800, pls 97–104.

Sanders, H. L. 1963. The Cephalocarida. Functional morphology, larval development, comparative external anatomy. *Mem. Conn. Acad. Arts Sci.*, New Haven, **15** : 1–80.

Salter, J. W. 1864. A monograph of British trilobites. **1** : 1–80, pls 1–6. *Palaeontogr. Soc.* (*Monogr.*), London.

Stubblefield, C. J. 1926. Notes on the development of a trilobite, *Shumardia pusilla* (Sars). *J. Linn. Soc.*, London, (Zool.) **36** : 345–372, pls 14–16.

—— **& Bulman, O. M. B.** 1927. The Shineton Shales of the Wrekin District: with notes on their development in other parts of Shropshire and Herefordshire. *Q. Jl geol. Soc. Lond.* **83** : 96–146, pls 3–5.

Westergård, A. H. 1922. Sveriges olenidskiffer. *Sver. geol. Unders. Afh.*, Stockholm, (Ca) **18.** 205 pp., 16 pls.

—— 1946. Agnostidea of the Middle Cambrian of Sweden. *Sver. geol. Unders. Afh.*, Stockholm, (C) **477.** 140 pp., 16 pls.

Whittington, H. B. 1965. Trilobites of the Ordovician Table Head Formation, western Newfoundland. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **132** : 281–441, 68 pls.

—— **& Evitt, W. R.** 1954. Silicified Middle Ordovician trilobites. *Mem. geol. Soc. Am.*, New York, **59** : 1–137, 33 pls.

Wiman, C. 1905. Ein Shumardiaschiefer bei Lanna in Nerike. *Ark. Zool.*, Stockholm, **2** (11) : 1–20, 2 pls.

Pleistocene bird remains from Tornewton Cave and the Brixham Windmill Hill Cave in south Devon

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Synopsis

Avian fossil material has been found in Tornewton Cave and the Windmill Hill Cave at Brixham, both in south Devon, England. The Tornewton material originates from strata deposited during an early cold phase, followed by an Ipswichian warm phase and by cold Devensian phases. The Brixham Cave material is Devensian in age. Twenty-two bird species are identified, including a new species of small partridge *Alectoris sutcliffei*. The abundant remains of the Shelduck *Tadorna tadorna* are thought to have been prey of the White-tailed Sea-eagle *Haliaeetus albicilla*, and their absence from Tornewton in the Devensian may be because of the absence of the predator rather than the prey species. Because many species are migratory, birds are often poor indicators of climatic conditions. Apart from the presence of Ptarmigan *Lagopus mutus* in the Devensian, the tundra species are absent. It is suggested that parts of the area may have carried a more boreal flora during the cold periods, and that the area may have benefited from the proximity to the sea which may have had some modifying effect on climatic conditions.

Introduction

The caves of south-west England have yielded a large quantity of late Pleistocene remains of mammals and birds, with the former in greater abundance. Unfortunately in some caves an accidental admixture of earlier deposits with Recent material during the later stages of deposition or during animal or human occupation, and the collecting of some specimens in the last and the early part of the present centuries without due regard to stratification of the cave floor, have made the contents of these caves of limited value in the study of faunal succession at different periods.

Tornewton Cave is an exception in that careful collecting of material during nearly two decades makes it possible to study a succession of specimens dating from the last, Devensian glaciation back through a warm period of the Ipswichian interglacial to a preceding cold period (Sutcliffe & Zeuner 1962). This cave provides the main mass of material, and the more limited material from the Windmill Hill Cave has been included because this is from the last glaciation, of Devensian age, and supplements the information provided by the Tornewton specimens for this period. All the material consists of dissociated bones, and mainly of the ends of the larger limb bones.

All the specimens referred to are in the collection of the Department of Palaeontology of the British Museum (Natural History); numbers prefixed with A or without prefix. The Windmill Hill Cave at Brixham was excavated by W. Pengelly in 1858–9 and the specimens collected were presented, mainly by the Royal Society, in 1876. The Museum purchased from F. H. Butler part of the collection made by J. L. Widger at the Tornewton and other Torbryan Caves (Walker & Sutcliffe 1967) in 1892, and the eagle claws from this have been included. The remaining extensive Tornewton material was collected in the period 1944–69 and presented by the late Mr S. R. Willing.

The Brixham Cave specimens were identified by Lydekker (1891). Some of the earlier Tornewton material had been identified by Miss P. Lawford in 1955, and some Glutton Stratum bones by D. Bramwell in 1961. The material from this cave had also been examined more recently by Dr J. Janossy of Hungary. For the present paper the material was critically re-examined and compared with Recent osteological specimens in the Sub-department of Ornithology, British Museum (Natural History) and reidentified where necessary.

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Sites and strata

Tornewton Cave is one of a series of caves in the limestone on the west side of the Torbryan Valley in south Devon. It is about 250 ft (76 m) above sea level, and about five miles (8 km) from the sea at Torbay to the east of it, and about six and four miles (9·5 and 6·5 km) from the upper ends of the estuaries of the rivers Teign and Dart respectively. The Windmill Hill Cave at Brixham is on a hillside bordering the coast on the south side of Torbay, the cave now being within the town of Brixham. The position of the coastline would have differed from that of the present day during the various cold and warm periods of the Pleistocene. In cold periods it would have been much further away, and maps reconstructing the distribution of the icefields sometimes tentatively indicate a coastline from south-western Ireland to beyond Brittany. From the present altitude of the surrounding areas, in warm periods the coast might not have been much closer to the cave than it is at present. However, the preponderance of Shelduck bones in most strata of the caves implies that conditions suitable for this species were present no further away than the distance which a predator was likely to transport them. Unless their ecological requirements differed significantly at this period, Shelduck would have required saline or brackish mudflats on which to feed, such as usually occur along estuaries or around lagoons with fluctuating water levels.

The sequence of deposits in Tornewton Cave has been studied and named with reference to the mammal fauna (Sutcliffe & Zeuner 1962). Both the mammal remains and the nature of the deposits indicate that the latter were laid down in several different climatic periods. They commence in an earlier cold period, which is overlain by a more typically warm Ipswichian deposit, and the most recent of the Tornewton deposits are from the last, Devensian, glaciation. The whole series of deposits referred to in the present paper, beginning with the earliest, is as follows.

Tornewton Cave

Glutton Stratum (? late Wolstonian or later cold phase). This deposit, so named because it contains remains of the Wolverine or Glutton, *Gulo gulo*, was laid down during a cold period with a severe climate and also contains remains of other northern mammals such as Reindeer, *Rangifer tarandus*. This may have been the later stage of the Wolstonian (penultimate) glaciation, but since there may have been one or more cold stages in the last interglacial interval (Shackleton 1969, 1977; Sutcliffe 1975, 1976; Woillard 1978) this cannot be established with certainty.

Bear Stratum (? late Wolstonian or later cold phase). This has a similar fauna to the Glutton Stratum, but with some evidence from the nature of the deposits of an ameliorating climate, cool but not as cold as the previous one.

Otter Stratum (?). This stratum occurs in a small side chamber of the cave. The otter referred to is the extinct clawless otter *Cyrnaonyx antiqua*, also occurring in the Glutton Stratum but not otherwise known in Britain. The stratum appears to consist of a mixture of two deposits, one warmer and the other cooler, and to have been deposited in a period between the Glutton Stratum and Hyaena Stratum depositions, with elements of both (Sutcliffe & Kowalski 1976).

Hyaena Stratum (Ipswichian Interglacial). The fauna is that of a warm interglacial period.

Reindeer Stratum (Devensian). The mammalian fauna of this period indicates a return to glacial conditions; Man was present. An earlier Devensian cold stage is represented at the cave by 'the Head', a deposit from which no bird material has been collected.

'*Eboulis*' (Devensian). The position of this deposit in the sequence of strata is not completely certain, but it may represent another later phase.

Windmill Hill Cave, Brixham

(Devensian). The material from this cave has not been assigned to a series of strata.

The bird species identified, dating from the Devensian glaciation back to an earlier cold phase, have been tabulated by strata (Table 1); to aid comparison the occurrences for the earlier and later cold periods have, in addition, been grouped in single columns on either side of the list for the single warm period between.

Table 1 Occurrence of species identified

Species	Glutton Stratum (cold)	Glutton/ Bear (cold)	Bear Stratum (cool)	Otter Stratum (?)	Combined early (cold)	Hyaena Stratum (warm)	Combined Late (cold)	Reindeer Stratum (cold)	'Eboulis' Stratum (cold)	Brixham Cave (cold)
? White Stork	×	×	×	–	×	–	–	–	–	–
Brent Goose	–	–	–	×	×	×	–	–	–	–
? Ruddy Shelduck	–	–	–	–	–	×	–	–	–	–
Common Shelduck	×	×	×	×	×	×	×	–	–	×
Wigeon	–	–	–	–	–	×	–	–	–	–
Teal	–	–	–	–	–	–	×	×	–	–
Goosander	×	–	–	×	×	–	–	–	–	–
White-tailed Sea-eagle	–	–	?×	–	?×	–	–	–	–	–
Common Buzzard	–	–	–	–	–	–	×	–	–	×
Kestrel	×	–	–	–	×	×	–	–	–	–
Ptarmigan	–	–	–	–	–	–	×	×	×	–
Willow Grouse	–	–	–	–	–	–	×	×	–	–
Western Partridge (sp. nov.)	×	–	–	–	×	–	–	–	–	–
Little Bustard	–	–	–	–	–	–	×	×	–	–
Eagle Owl	×	–	–	–	×	–	–	–	–	–
Skylark	–	–	–	–	–	×	×	×	–	–
Tree Pipit	–	–	–	–	–	×	–	–	–	–
Fieldfare	–	–	–	–	–	–	×	×	–	–
Crossbill	×	–	–	–	×	–	–	–	–	–
Starling	–	–	–	–	–	×	×	×	–	–
Carrion Crow	–	×	–	–	×	–	×	×	–	–
Raven	×	–	–	–	×	×	–	–	–	–

Systematic list of material

? White Stork, *Ciconia ? ciconia*. Two very similar species of stork occur in the Palaearctic today, the White Stork and the Black Stork *C. nigra*. Both occur in marshy habitats, the former in more open country and the latter in forest. Osteologically they are very similar, but with some differences in the proportional lengths of limb bones. Since the fossil specimens are broken ends of bones these differences cannot be used. Three Recent *C. ciconia* specimens and two of *C. nigra* were available for comparison. The fossil specimens agree with those of *C. ciconia* in having on the distal end of the tibiotarsus a broader anterior tendinal canal and a narrower tubercle on the tendinal bridge.

The material comprises parts of carpometacarpi, radii, tarsometatarsi and tibiotarsi from the Glutton Stratum, a distal end of a tibiotarsus from the Glutton/Bear Stratum transitional zone and part of a radius from the Bear Stratum. A4095, A4110, A4117, A4118, A4135, A4143, A4166.

Brent Goose, *Branta bernicla*. Bone fragments of this species are sometimes difficult to separate from those of *Tadorna* spp., but the present specimens can be assigned to it. The material comprises parts of tarsometatarsus and humerus from the Otter Stratum and parts of carpometacarpus, ulna and radius from the Hyaena Stratum. A4107, A4127, A4154, A4157.

Common Shelduck, *Tadorna tadorna*. Bones referable to this species form the major part of the whole collection. When Lydekker (1891) examined the Brixham material he does not appear to have used a specimen of this species for comparative purposes, although one was present in the Museum collection at the time. He compared the bones with those of the Ruddy Shelduck *T. ferruginea* and the South African Shelduck *T. cana*. He seemed unaware that there is a strong sexual dimorphism in the present species, the female being smaller, and he suggested that the smaller specimens represented a new species. Possibly because of these comments most of the shelduck material in the collection of the Department of Palaeontology had been tentatively assigned to *T. ferruginea*. Skeletons of three *T. tadorna* and five *T. ferruginea* were available for comparison. Differences in the limb-bones are slight, but in general *T. tadorna* has shorter and stouter bones and, with one exception, where differences were apparent the material was referred to this species. Humerus, tarsometatarsus and to a lesser degree the femur are the most useful bones for comparative purposes.

From the Tornewton Cave the material comprises tarsometatarsi, tibiotarsi, femora, coracoids, humeri, radii, ulnae, carpometacarpi, anterior ends of sterna, and furcula from the Glutton Stratum; tarsometatarsi, tibiotarsi, coracoids, humeri, ulnae, carpometacarpi, sacrum and vertebrae from the Glutton/Bear Stratum transitional zone; tarsometatarsi, femora, coracoids and ulna from the Bear Stratum; tarsometatarsi, tibiotarsi, femora, coracoids, humeri, radii, ulnae and carpometacarpus from the Hyaena Stratum; and tarsometatarsi, tibiotarsi, coracoids, ulnae and carpometacarpi from the Otter Stratum. A4091–3, A4096–7, A4099–4101, A4108, A4113–6, A4136, A4155–7, A4162–4, A4170, A5033–4, A5036.

From the Windmill Hill Cave, Brixham, we have tarsometatarsi, tibiotarsi, femora, coracoids, scapulae, humeri, ulnae, radii, carpometacarpi, metacarpal, anterior ends of sterna, furcula and vertebrae. 48911, 48915, A113, A3138–48, A3150–74, A3179–81.

? Ruddy Shelduck, *Tadorna ? ferruginea*. As mentioned above, there are difficulties in separating the bones of the two *Tadorna* species. The present specimen is a femur from the Hyaena Stratum, A5037, which is longer and proportionally more slender than any in the available skeletons of *T. tadorna*; it matches that of a male *T. ferruginea*. Specimens collected at the same time from the same stratum are referable to *T. tadorna*.

Wigeon, *Anas penelope*. Coracoid and part of a carpometacarpus from the Hyaena Stratum. A4111, A4124.

Teal, *Anas crecca*. Femur, carpometacarpus and part of a humerus from the Hyaena Stratum. A4104, A4121, A4122.

Goosander, *Mergus merganser*. Parts of humeri from the Glutton Stratum and parts of tibiotarsi and coracoids from the Otter Stratum. A4198, A4138, A5035.

White-tailed Sea-eagle, *Haliaeetus albicilla*. Claws, A233, collected by J. L. Widger and received with other Widger specimens, are merely labelled 'Torbryan Caves' but are very probably the ones referred to in his account (Walker & Sutcliffe 1967 : 80) as 'claws of an immense bird' and collected in the Bear Stratum of Tornewton Cave. There is also a single claw, A4141, from the Tornewton cave but from unstratified material.

Common Buzzard, *Buteo buteo*. It is possible that the Rough-legged Buzzard *B. lagopus* may have occurred in this region in colder periods in view of its typical climatic and habitat preferences, but the present material is referable to the smaller *B. buteo*, the specimens matching those of the smaller male of this dimorphic species. The material comprises parts of humerus, ulna, carpometacarpus and pelvis from the Windmill Hill Cave, Brixham. 48913, 48917, A3149.

Kestrel, *Falco tinnunculus*. Parts of ulna and tarsometatarsus from the Glutton Stratum; coracoid, carpometacarpus and ulna from the Hyaena Stratum. A4133, A4149–51, A4159.

Ptarmigan, *Lagopus mutus*. Several bones of this species are present, but the characteristic tarsometatarsi are a little smaller than those of Recent specimens. The material comprises parts of tarsometatarsi and coracoid from the Reindeer Stratum outside the cave, and part of a carpometacarpus from the 'Eboulis' deposit. A4125, A4147, A4148.

Willow Grouse, *Lagopus lagopus*. A tarsometatarsus from the Reindeer Stratum outside the cave. A4106.

Western Partridge, *Alectoris sutcliffei* sp. nov. See p. 96.

Little Bustard, *Otis tetrax*. Part of a carpometacarpus from the Reindeer Stratum outside the cave. A4112.

Eagle Owl, *Bubo bubo*. Although incomplete the specimen agrees in size with the larger northern Recent form of this species, whereas that from the earlier Cromer Forest Bed Series of East Anglia (Harrison 1979) is similar to the smaller southern Recent form. The material is an ungual from the Glutton Stratum. A4169.

Skylark, *Alauda arvensis*. An ulna, humeri and coracoid from the Hyaena Stratum; humeri, coracoids and carpometacarpi from the Reindeer Stratum. A4102, A4103, A4134, A4152.

Tree Pipit, *Anthus trivialis*. There is little osteological variation among the pipits. Material is part of a humerus from the Hyaena Stratum. A4123.

Fieldfare, *Turdus pilaris*. A coracoid from the Reindeer Stratum. A4192.

Crossbill, *Loxia* cf.*curvirostra*. The specimen resembles the corresponding bone of *L. curvirostra*, and is smaller and less stout than that of *L. pytyopsittacus*. *L. scoticus* is intermediate in general size between these two, and the Asiatic *L. leucoptera* is smaller than *L. curvirostra*, but comparative osteological material is not available. The breeding distribution of northern European crossbills is broadly linked with the occurrence of either Spruce or Pine trees, though birds may at times take seeds of either as well as of other conifers. Nethersole-Thompson (1975) has suggested that crossbills speciated from an ancestral form when their original principal foodsource, the Spruce *Picea abies*, ceased to occur, to produce the Scottish Crossbill *L. scoticus* and the Parrot Crossbill *L. pytyopsittacus* in Scandinavia and northern Russia, both specializing mainly on the seeds of the Scots Pine *Pinus sylvestris*. Further east the Common Crossbill *L. curvirostra* persisted as a specialist mainly on Spruce. The latter tree did not re-invade Europe after the last glaciation until after the isolation of the British Isles, where neither tree nor bird is native, although the first has been introduced and the latter has recently re-invaded and now breeds. From the evidence of pollen deposits Spruce did occur in Britain through the Pleistocene until the Lower Wolstonian, although in smaller proportions than other forest trees, and later as a scarce and probably localized tree in Ipswichian to Lower Devensian times, but not subsequently

(West 1977). The present specimen might therefore have been co-extant with Spruce in south-west England, and its normal existence was certainly correlated with the presence of conifers. The material is part of a humerus from the Glutton Stratum. A4128.

Starling, *Sturnus vulgaris*. On average these bones are slightly larger than those of Recent specimens. Two of the humeri are atypical in lacking the anconal fossa near the proximal end of the shaft. Carpometacarpi, ulnae, humeri, coracoid and femora are from the Hyaena Stratum; femora, coracoids, humeri, ulnae and carpometacarpi are from the Reindeer Stratum. A4105, A4130, A4139, A4140, A4144–6.

Carrion Crow, *Corvus corone*. The bones are towards the larger end of the size range of the species and the tibiotarsus shaft is stout. We have part of a tibiotarsus from the Glutton/Bear transitional zone and part of a femur from the Reindeer Stratum outside the cave. A4109, A4126.

Raven, *Corvus corax*. Parts of humeri, tibiotarsus and tarsometatarsus from the Glutton Stratum; ulna and parts of coracoids, tibiotarsus and tarsometatarsus from the Hyaena Stratum. A4031, A4044, A4119, A4120, A4132, A4142, A4160, A4161.

Systematic description

Order **GALLIFORMES**

Family **PHASIANIDAE**

Genus ***ALECTORIS*** Kaup, 1829

Alectoris sutcliffei sp. nov.

Western Partridge; Fig. 1

Diagnosis. Small, distal end of tibiotarsus smaller than that of any known *Alectoris* species.

Name. After Dr A. J. Sutcliffe, who has worked extensively on Pleistocene mammal remains and was responsible for assembling most of the present material.

Material. Holotype the distal end of a left tibiotarsus, collected by A. J. Sutcliffe in 1960; BM(NH) no. A4165. Tentatively referred specimen a distal end of a tibiotarsus (illustrated as a left-hand bone, but described in the caption as from the right) described by C. Mourer-Chauviré (1975) as '*Alectoris* sp.'.

Occurrence. Holotype from the Upper Middle Pleistocene; Glutton Stratum, Tornewton Cave, Torbryan, Devon, England. Tentatively referred specimen from ? Gunz glaciation, Early Middle Pleistocene; Mas Rambault à Frontignan, Hérault, southern France.

Description and discussion. The specimen is the distal end of a tibiotarsus of a small phasianid gamebird. It had tentatively been identified as that of a Common Partridge *Perdix perdix* but it is stouter with less anteriorly-prominent condyles and a wider and more anteroposteriorly-flattened shaft. It matches the tibiotarsi of *Alectoris* species but is smaller. Its width is 6·5 mm and that of the French specimen, calculated from the scale provided, is *c*. 6·75 mm. For the Red-legged Partridge, *A. rufa*, comparable measurements are 7·2–7·3 mm (5 specimens) and for the Rock Partridge *A. graeca*, Barbary Partridge *A. barbarae* and Chukar *A. chukar* they range from 7·4 to 8·5 mm (11 specimens). The species is therefore distinctly smaller than others of this genus. Mourer-Chauviré (1975) recognizes *A. graeca* and *A. barbarae* from cave deposits in southern France back to the Mindel glaciation, but finds no evidence of *A. rufa* which is now the native species of most of southern France. It is possible that the latter is derived from an Iberian isolate of fairly late glacial origin. The western zone of the range of *Alectoris*, including the southern site of *A. sutcliffei*, is now occupied by *A. rufa*, but the extinct *sutcliffei* occurred further north, and in a colder period, and must have been more tolerant of low temperatures.

Measurements (in mm). Length of specimen 12·4; distal width 6·5; anteroposterior thickness of internal condyle 6·4, of intercondylar groove 3·8, of external condyle 5·8; width and thickness of shaft 4·5×2·7; distoproximal width of tendinal bridge 2·1.

The avian predators

The range of prey species found in caves is determined by the species of predator which fed there, and from the specimens examined in the present study it seems likely that avian predators were responsible for introducing most or all of the bird remains; they tend to leave bird bones relatively complete whereas mammalian predators tend to splinter and destroy them. Avian predators also tend to have a preferred prey size which may limit their range of prey significantly, and they may concentrate on some easily available species.

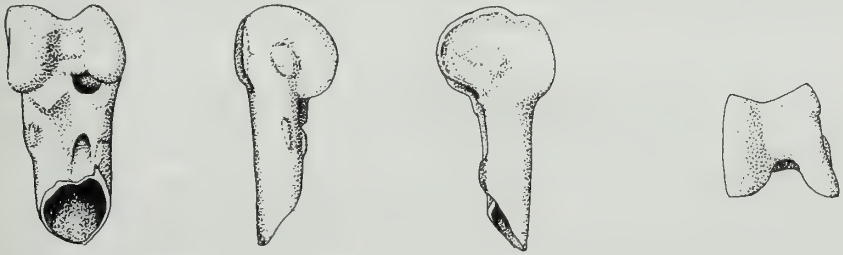

Fig. 1 *Alectoris sutcliffei* sp. nov. **Holotype**, distal end of left tibiotarsus, BM(NH) no. A4165. (Left to right) distal, internal, external, anterior views.

The predominant bird bones found were those of the Common Shelduck. This species presents two problems; it is a large and heavy prey for an avian predator, and a bird of estuaries and coasts. The coast is at present several miles from Tornewton Cave and is unlikely to have been much nearer the cave in the past. The Shelduck feeds on tidal mudflats. Although it may fly inland to utilize concealed nest sites, it is doubtful if this would explain the number of fossil remains. The presence at the same period of the Brent Goose, a similar large species of tidal mudflats, and possibly of the Wigeon which also occurs on this type of habitat in winter, tends to support the suggestion of a predator hunting along the shore.

Foxes and wolves were present at the time, but even if they could produce the type of specimens found, it seems unlikely that mammalian predators of this type would be persistently successful in killing Shelduck, or would have transported them for long distances overland. Two avian predators large enough to have taken such prey are known from the Tornewton Cave – the Eagle-owl and the White-tailed Sea-eagle. The former is unlikely to have moved very far from the cave to hunt, and may have concentrated mainly on mammalian prey. The Sea-eagle, however, usually hunts and scavenges on seacoasts, taking numbers of ducks and larger waterfowl. The Shelduck, which is conspicuous at a distance, feeds on mudflats where it cannot dive to avoid a winged predator, and is fairly slow to take flight, would be a natural prey for the eagle. Sea-eagles are not normally cave-nesters and it is not obvious how they would have utilized the Tornewton site. It is possible that the rock platform at the top entrance might have formed a nest site from which food and pellets could have fallen into the cave.

Shelduck remains, although numerous from the Glutton to the Hyaena Strata at Tornewton, are suddenly absent in the Devensian. This could suggest a change in species distribution, but since prey remains in caves are determined by the species of raptor present it could alternatively indicate a change in the latter. The Brixham Devensian material consists almost entirely of Shelducks, indicating that the species was certainly present for at least part of this period. An absence of the Sea-eagle from Tornewton Cave in the Devensian period, possibly coincident with the use of the cave by man, is likely to have been why the Shelduck bones are absent, rather than a temporary absence of the latter species from this region. Since the larger prey are typical of the Sea-eagle it may be significant that during the Devensian the only waterfowl remains at Tornewton are those of the very small Teal.

The Common Buzzard of the Brixham Cave may have been there by accident or as a prey item rather than a predator. It is just possible that this species might have utilized a cave in a very bare and windswept biotope, but in inland areas it would normally have used trees where these were available, or the ledges of larger rock outcrops, for roosting and nesting.

The Kestrel was present at Tornewton in the earlier cold period and the interglacial and may well have been responsible for the presence of small passerine bird remains as well as those of small mammals. Other species of falcon tend to concentrate almost entirely on birds. Other raptors which produce small bird bones in prey remains are the small to medium-sized owls, of which there is no evidence in the material from Tornewton, although the presence of the remains of prey without those of the predator is not unusual where birds are concerned. There are no Kestrel remains from the Devensian strata but the presence of small passerine remains from this period suggests that this or a similar smallish raptor was present.

The species list as evidence of climate

Since there is evidence of climatic variation from one stratum to another in this cave material, and since this is reflected in the mammal species present, similar changes in the bird fossils could be expected. In fact, within this group the situation is more complicated because of the greater mobility of birds. Resident bird species give some indication of the conditions at the time, but within this region the majority of birds are partly or wholly migratory. The presence during a cold period of a species which can tolerate the warmer summer conditions, combined with the presence in a warmer period of cold-adapted species wintering in the area, can seriously confuse the general picture which bird fossil may provide. There is some evidence of this problem in the present material.

Of the species present in the earlier cold Glutton to Otter Strata, the White-tailed Sea-eagle, Kestrel, Eagle-owl, Crow and Raven are now resident from the temperate zone at least as far as the northern edges of the Boreal forest zone and may extend into wooded tundra (climatic zones as in Voous 1960). The Brent Goose and Goosander have a similar range but make a more southerly shift to warmer boreal and temperate parts in winter. The Shelduck has a mainly warm temperate distribution at the present time but on the eastern Atlantic seaboard extends north to northern Norway. This is correlated with the presence of the warm North Atlantic Drift current modifying sea and shore temperatures, although in the Scandinavian part of its range the species is only a summer visitor. The Western Partridge is a member of a genus of gamebirds normally found in warm temperate to temperate zones, although the Rock Partridge and Chukar will ascend to fairly high altitudes.

The two stork species are now summer visitors to Europe, nesting as far north as northern Denmark and the Gulf of Finland, and Voous (1960) suggests that the northern limit of their range is correlated with the July isotherm of 62 °F (16·7° C). The final species recorded for this period is the Crossbill, and the occurrence of this species, unless it was a dying stray from some irruptive movement, would indicate the nearby presence of conifer trees.

If it is reasonable to view this material as an entity, it suggests that during this early cold period the surroundings of the cave might have resembled present-day southern Scandinavian boreal conditions, with the presence of some conifer trees and a mid-summer temperature of *c.* 62 °F. However, the winters might have been more severe (Sutcliffe & Zeuner 1962).

The species present in the Hyaena Stratum in the warmer interglacial are disappointing as climatic indicators. The list could be one indicating birds now present in a temperate zone in winter or a boreal zone in summer. The only exception is the tentatively-identified Ruddy Shelduck. This is mainly a species of drier steppe regions. The Starling may have roosted and nested in the cave. The presence of both the latter species and the Skylark suggests that some open grassland was present nearby.

For the Devensian period, the presence of the Arctic/Alpine Ptarmigan indicates more definitely a colder climate. The Willow Grouse might have been the typical bird of cold willow and birch scrub, or possibly a Red Grouse form adapting to heather moorland. The grassland Starling and Skylark were still present. Of the remaining species, Teal, Fieldfare and Crow are all species that might occur from temperate to subarctic conditions, but are not tundra birds. The exceptional occurrence is the Little Bustard. This is a warm temperate species, extending into temperate regions in summer, and at present just reaching northern France. It is, however, partly a migrant, and it is possible that the Tornewton specimen was a stray individual that had overshot its usual range at that time. At Brixham, the combination of Common Buzzard and Shelduck suggests boreal rather than tundra conditions.

Sutcliffe & Kowalski (1976) have over 2000 specimens of rodents from Tornewton Cave and with this more abundant material have produced a table of the relative proportions of the various groups of rodents, part of which is shown in Table 2. It will be seen that they also found evidence of boreal and forest species in the colder periods. Except for the presence of the Ptarmigan in the Devensian, the tundra element cannot be confirmed among the birds.

Table 2 Relative proportions of the various ecologic groups of rodents found in Tornewton Cave (from Sutcliffe & Kowalski 1976:66)

Layer	Tundra and steppe	Boreal	Forest	Neutral
Reindeer Stratum	22·9	8·7	5·5	62·8
Hyaena Stratum	0	0	2·3	97·7
Bear Stratum	25·8	48·4	9·6	16·1
Glutton Stratum	22·7	64·2	0·7	12·4

It is possible that the higher ground of Dartmoor and similar moorland areas could have carried a tundra-type fauna and flora when more sheltered areas of lower ground might have had a more boreal flora with some trees, as in parts of northern Scandinavia today. It also seems possible that this area of south-west England, on the southern side of higher ground and close to an oceanic shoreline, might have experienced, even under severe conditions and at different stages of sea-level, a more favourable climate compared with sites further inland on the continental landmass. These opposite tendencies could have resulted in a more varied fauna and flora at these earlier periods in this area.

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I am very grateful to my colleague Mr C. A. Walker who helped me to trace and assemble this material; to Dr A. J. Sutcliffe who provided much of the background information, and to Mr A. P. Currant and Dr C. B. Stringer who helped with further information and discussion.

References

Harrison, C. J. O. 1979. Birds of the Cromer Forest Bed Series of the East Anglian Pleistocene. *Trans. Norfolk Norwich Nat. Soc.* **25** : 277–286.

Lydekker, R. 1891. *Catalogue of the fossil birds in the British Museum (Natural History).* xxvii + 368 pp., 75 figs. London.

Mourer-Chauviré, C. 1975. Les oiseaux de Pléistocène Moyen et Supérieur de France. *Docums Lab. Géol. Fac. Sci. Lyon* **64** : 1–624; 22 pls, 72 figs, 89 tabs.

Nethersole-Thompson, D. 1975. *Pine Crossbills.* 256 pp., 17 pls, 18 figs, 17 tabs, 3 maps. Berkhamsted.

Shackleton, N. J. 1969. The last interglacial in the marine and terrestrial records. *Proc. R. Soc.*, London, B **174** : 135–154.

—— 1977. The oxygen isotope stratigraphical record of the late Pleistocene. *Phil. Trans. R. Soc.*, London, B **280** : 169–182.

Sutcliffe, A. J. 1975. A hazard in the interpretation of glacial-interglacial sequences. *Quaternary Newsl.*, Glasgow, **17** : 1–3.

—— 1976. The British glacial-interglacial sequence – reply to R. G. West. *Quaternary Newsl.*, Glasgow, **18** : 1–7.

—— **& Kowalski, K.** 1976. Pleistocene rodents of the British Isles. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **27** : 33–147; 31 figs, 13 tabs.

—— **& Zeuner, F. E.** 1962. Excavations in the Torbryan Caves, Devonshire. 1. Tornewton Cave. *Proc. Devon archaeol. Explor. Soc.*, Torquay, **5** : 127–145. 2 pls.

Voous, K. H. 1960. *Atlas of European birds.* 284 pp., 355 text photos, 419 maps. London.

Walker, H. H. & Sutcliffe, A. J. 1967. James Lyon Widger, 1823–1892, and the Torbryan Caves. *Rep. Trans. Devon. Ass. Advmt Sci.*, Plymouth, **99** : 49–110.

West, R. G. 1977. *Pleistocene geology and biology.* 2nd Edn. xi + 440 pp., 16 pls, 151 figs, 48 tabs. London.

Woillard, G. M. 1978. Grand Pile Peat Bog; a continuous pollen record for the last 140,000 years. *Quaternary Res.*, New York & London, **9** : 1–21.

The succession of *Hyracotherium* (Perissodactyla, Mammalia) in the English early Eocene

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Synopsis

In the light of recently-collected material and the documentation of old stratigraphical information, the English species of *Hyracotherium* are re-evaluated with a better knowledge of variation and diagnostic characters. A phylogeny is suggested and some correlations within Europe are proposed.

Introduction

The morphology of British *Hyracotherium* has been exhaustively treated by previous authors (Owen 1841, 1842, 1858; Cooper, C. F. 1932*b*; Simpson 1952) but two types of data, one old and one new, put it in a different perspective and produce somewhat different taxonomic and evolutionary conclusions. These data are a good knowledge of the stratigraphic position of most of the specimens, which had not previously been fully appreciated, and an increase in the number of specimens known from the Blackheath Beds and the Suffolk Pebble Beds by recent collecting, giving a better idea of the degree of variation and more reliable dental characters. Since Simpson's (1952) revision of British material new specimens have been collected, mainly from Abbey Wood, by S. A. Baldwin, D. Bone, J. Collins, J. Cooper, A. Gale, W. H. George, P. R. Gurr, K. J. Hall, R. A. D. Markham, A. R. G. Packman, P. R. Payne, D. J. Ward, K. Wright and the author.

The registered numbers of specimens in the various institution collections are indicated by the following prefix letters: British Museum (Natural History), London (M or no prefix); Sedgwick Museum, Cambridge (C); Ipswich Museum, Suffolk (IM); Muséum National d'Histoire Naturelle, Paris (MU, AV or AL); University of California Museum of Paleontology, Berkeley (UC).

Symbols used in synonymies as in Matthews (1973).

Stratigraphy

Simpson (1952 : 202), referring to the holotypes of *H. leporinum* and *H. vulpiceps*, stated: 'their relative levels within the London Clay have not been, and perhaps cannot be, established'. The horizon of the latter is recorded by Owen (1858 : 55) as the Roman Cement bed at Harwich (=Harwich cement stone (Davis & Elliott 1951 : 331) and the Harwich Stone Band (Elliott 1971)) which occurs 6 m above the base of the London Clay. This is now known to be an important ash marker (Elliott 1971) and is correlated with a Greenland volcanic episode dated at 53 Ma (Fitch *et al.* 1978). The lithology of the adherent matrix shows the quoted provenance to be correct. The age-equivalent deposit in Denmark, the Mo Clay, belongs to the calcareous nannoplankton zone 10.

The horizon of the holotype of *H. leporinum* is less accurately known but details of its collection from the cliff at Studd Hill, near Herne Bay, were given by Richardson (1841). Remains of the crinoid *Isselicrinus subbasaltiformis* (Miller) were formerly to be found (Cooper, J. 1977 : 173; Gamble 1979) about half-way up the cliff before the section was obscured by sea defences. This species has a restricted range in the London Clay between about 27 m and 37 m above the base (= Division 2 of Wrigley, 1924; King 1970). Its main occurrence at Studd Hill is restricted to 31–32 m above the base (Gamble 1979). The holotype of *Hyracotherium leporinum* evidently came from the vicinity of this horizon and thus occurs significantly higher than the holotype of *H.*

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vulpiceps. A second specimen of *H. leporinum* from the Herne Bay foreshore (C. B. Brown collection), now in the Sedgwick Museum, Cambridge, is most likely to be from the same horizon.

An imperfect cranium of *H. vulpiceps* (38801) is not, as quoted by Cooper, C. F. (1932*b* : 433) and Simpson (1952 : 195), from Sheppey but, according to the British Museum (Natural History) Palaeontology Department register, 'from the Crag (wreck of London Clay)'; i.e. from the Red Crag basement bed of Suffolk. This is of late Pliocene age but contains much material derived from the London Clay. The dark reddish, highly polished surface of the adherent matrix shows the quoted provenance to be correct. The original horizon in the London Clay is, of course, unknown but today only the lower part is preserved in Suffolk below the unconformity at the base of the Red Crag.

Further British specimens that have been attributed to *Hyracotherium* are two mandibular fragments without tooth crowns (38939, 47986; see Lydekker 1886 : 11) from the London Clay of Sheppey. They are generically indeterminable but the horizontal ramus (38939) is very similar to that of the holotype of *H. vulpiceps* in size and morphology. Further specimens would be very interesting in view of the later Cuisian age indicated by Costa & Downie (1976 : 600, 603) for this part of the succession.

Specimens, here identified as *H.* aff. *vulpiceps*, from Abbey Wood, occur in the Abbey Wood member of the Blackheath Beds which underlie the London Clay. The associated fauna is as follows:

Charlesmooria childei Kühne, 1969
? *Didelphodus* sp.
Didelphodontinae indet.
? *Eochiromys* sp.
? *Macrocranion* sp.
Adapisoricidae indet.
'*Adapisorex*' *anglicus* C. F. Cooper, 1932*a*
Phenacolemur cf. *fuscus* Russell, Louis & Savage, 1967
Teilhardina sp.
Pelycodus eppsi (C. F. Cooper, 1932*a*)
Esthonyx sp.
Microparamys sp.
Paramyidae indet.
? *Prototomus* sp.
Oxyaena sp.
Arctocyonidae indet.
Hyopsodus wardi Hooker, 1979
Lessnessina packmani Hooker, 1979
? *Phenacodus* sp.
Coryphodon eocaenus Owen, 1846
Hyracotherium aff. *vulpiceps* (Owen, 1858)
Protodichobune sp. 1

The specimens of *H. cuniculus* from Kyson came from the Suffolk Pebble Beds, which immediately underlie the London Clay in Suffolk, and further specimens are here recorded for the first time from the same beds at Bramford and Ferry Cliff. The Suffolk Pebble Beds have often been synonymized or equated in age with the Blackheath or Oldhaven Beds because of their identical position below the London Clay and their superficial lithological similarity. However, their mammal fauna is different from that of Abbey Wood, its overall aspect being more primitive and rather similar to those of Dormaal and Erquelinnes, Belgium (Quinet 1969; Gingerich 1976 : text-fig. 18). The fauna is as follows (locality initials indicated for Bramford, Ferry Cliff, Harwich and Kyson):

Leptictidae indet.	K, FC
Paschatherium dolloi (Teilhard de Chardin, 1927)	FC

Plesiadapis aff. *remensis* Lemoine, 1887	K
P. aff. *tricuspidens* Gervais, 1877	FC
Omomyidae indet.	FC
Pelycodus sp.	K
Paramys sp.	K, FC
Meldimys sp.	FC, ? H
? *Prototomus* sp.	K
Creodonta indet.	K
Miacidae indet.	K
Landenodon sp.	K, FC, H
Microhyus musculus Teilhard de Chardin, 1927	K, FC, H
Hyopsodus cf. *wardi* Hooker, 1979	K
? *Coryphodon* sp.	FC
Hyracotherium cuniculus Owen, 1842	K, FC, B
Protodichobune sp. 2	K

Boswell (1916 : 571) stated: 'the lithology and petrology of the pebble bed suggests that it should be grouped with the Reading Beds, but its fauna is a typical London Clay assemblage'; but also (1916 : 566) 'unfortunately the species [molluscs and fish] are of rather wide range, and are not sufficient to form the basis of any correlation'. The Suffolk Pebble Beds (White 1931 : 40) are here accepted as distinct from the Blackheath or Oldhaven Beds, and somewhat older. The stratigraphical evidence for the English *Hyracotherium* succession is shown in the geological columns in Fig. 6, p. 111.

Morphology

Most authors have agreed on the separation of at least two English *Hyracotherium* species on the basis of size (smaller *H. cuniculus* and larger *H. leporinum* and *vulpiceps*), but opinions on the validity of the separation of the two larger ones have varied (see synonomy lists). Simpson (1952 : 202) found the teeth to vary so much that 'no other specimens show exactly the same distinction as these types [the holotypes of *H. leporinum* and *H. vulpiceps*] and none can be referred with real clarity to one species rather than the other'. In the stratigraphically-controlled assemblages mentioned above certain characters do in fact show a distinctness which can be used for specific separation. On the other hand, additional specimens from Abbey Wood strengthen Simpson's (1952 : 202) view of the variability of other characters such as the lingual cingulum. The characters found to be of low variability and useful in separating species and recognizing trends are as follows:

1. Configuration of upper molar centrocrista (and to a certain extent the presence of a mesostyle)
2. Structure and size of M_3 hypoconulid lobe
3. Shape and structure of P^3
4. Overall size of teeth.

Features of the skull discussed in detail by Simpson (1952 : 196–200) and Savage *et al.* (1965 : 49–50) are not considered here because they are known for only two specimens (one each of *H. leporinum* and *H. vulpiceps*) and their variability cannot be assessed.

Systematic descriptions

Family **EQUIDAE** Gray, 1821

Genus ***HYRACOTHERIUM*** Owen, 1841

1841 *Hyracotherium* Owen : 203–208.
1846 *Macacus* Desmarest; Owen : 1–10.
1858 *Pliolophus* Owen : 54–71; pls 2–4.
1876 *Eohippus* Marsh : 401.

1880 *Lophiodochoerus* Lemoine : 589 (*fide* Teilhard de Chardin 1922 : 67).
1896 *Protorohippus* Wortman : 92, figs 14–15.

TYPE SPECIES. *Hyracotherium leporinum* Owen, 1841.

REMARKS. The most recent generic diagnosis (Kitts, 1956) is evidently unsatisfactory as the type species tends to have a weak upper molar mesostyle and *H. vulpiceps* either has no $P\frac{1}{1}$–$P\frac{2}{2}$ diastema or this feature is intraspecifically variable. A revised diagnosis should await a full revision of the North American species.

Hyracotherium cuniculus Owen, 1842

Fig. 1a–c

v 1839 *Macacus*; Wood : 444–445, text-fig. 57.
v 1839 Macacidae; Owen : 446–448, text-fig. 58.
v* 1842 *Hyracotherium Cuniculus* Owen : 1–2, text-figs 2, 5.
v 1846 *Macacus eocaenus* Owen : 1–10, text-figs 1, 3.
v 1927 *Hyracotherium* sp.; Teilhard de Chardin : 27–28, text-fig. 28c; pl. 5, fig. 22.
v 1932*b* *Hyracotherium cuniculus* Owen; C. F. Cooper : 438–441, text-figs 1A, C, 2B, E, F; pl. 51, figs 6–9.
v 1952 *Hyracotherium cuniculus* Owen; Simpson : 196–204, text-fig. 4B.

TYPES. The left M^3, 36569 (Owen 1842 : text-fig. 2, reversed) was chosen as lectotype by Simpson (1952 : 196). One of the figured paralectotypes, the right $M^{1/2}$ M29709 (re-registered from 36569; Owen 1842 : text-fig. 5, reversed), is correctly identified. The distal half of a left $M^{1/2}$ M14111 (reregistered from 36572) may be Owen's unfigured paralectotype. Owen's supposed upper premolar (1842 : text-fig. 4, third paralectotype) looks most like M29699, which is a right M^2 of *Landenodon*.

OTHER MATERIAL. This is listed in the table of measurements, Table 1.

TYPE HORIZON AND LOCALITY. Suffolk Pebble Beds of Kyson, near Woodbridge, Suffolk (Nat. Grid TM 270475; see Prestwich 1850 : 272–273).

RANGE. Suffolk Pebble Beds of Bramford (TM 130477; Cooper, J. 1976) and Ferry Cliff near Woodbridge (TM 278486; George & Vincent 1976 : 25), both Suffolk. Also the Sables d'Erquelinnes of Erquelinnes (=Jeumont), Hainaut, Belgium (Rutot 1881).

EMENDED DIAGNOSIS. Small species of *Hyracotherium* (see Table 1), length of P^2–M^3 estimated 35 mm. Upper molars with straight centrocrista and no trace of a mesostyle. Lower molar metalophids tend to join trigonids nearer to protoconids than to metaconids. M_3 hypoconulid lobe small, tending to be buccal in position. P^3 with small protoconule; centrolingually placed protocone; straight mesiolingual margin; no postprotocrista.

DISCUSSION. Five individuals with lower molars and specifically four M_3s, four upper molars and two P^3s are available from the Suffolk Pebble Beds to demonstrate the constancy of the diagnostic characters. The right M_3 figured by Teilhard de Chardin (1927 : pl. 5, fig. 22) from Erquelinnes fits *H. cuniculus* in size and morphology as this author noted. According to Quinet & Verlinden's (1970) measurements, the Erquelinnes mandible figured first by Rutot (1881) is too big for *H. cuniculus*, being about the size of *H. vulpiceps*, but the metalophid joins the trigonid just buccal to the midpoint, more like *H. cuniculus* than *H. vulpiceps*. The small diastema between P_1 and P_2 is probably of little taxonomic value.

Hyracotherium vulpiceps (Owen, 1858)

Fig. 3a–c

v* 1858 *Pliolophus vulpiceps* Owen : 54–71; pls 2–4.
v 1865 *Hyracotherium leporinum* Owen; Owen : 340; pl. 10, fig. 2.
v 1886 *Hyracotherium leporinum* Owen; Lydekker : 11.

Table 1. Maximum length (l) and width (w) measurements (mm to the nearest 0·1) of English *Hyracotherium*. The following localities are indicated by their initials: Bramford, Ferry Cliff, Kyson, Abbey Wood, Harwich, Herne Bay, Suffolk (Red Crag basement bed). L = left, R = right.

Hyracotherium cuniculus

Number	Locality	tooth	l	w	Number	Locality	tooth	l	w
M14112	K	LP^{3}	(4·4)	5·2	M29701	K	LM$_{1/2}$	–	3·9
36572	K	LP^{3}	5·1	5·6	M36494	FC	RM$_{2}$	7·3	5·1
M29709	K	RM$^{1/2}$	(6·3)	8·1			RM$_{3}$	(8·8)	4·6
M14111	K	LM$^{1/2}$	–	(6·4)	M36495	FC	RM$_{1/2/3}$	–	5·0
M36496	FC	LM$^{1/2}$	6·6	–	M29710	K	RM$_{3}$	8·7	4·7
IM 1971-169	B	LM$^{1/2}$	7·5	–	M14113	K	RM$_{3}$	8·5	4·9
36569	K	LM^{3}	6·4	7·6	IM 1951-28-25	K	RM$_{3}$	8·4	4·8

Hyracotherium* aff. *vulpiceps

M13761	AW	RP^{3}	6·0	6·8	M29646	AW	LDP^{3}	5·4	–
		RP^{4}	6·7	8·1	M13763–4	AW	RDP$_{4}$	6·9	4·5
		RM^{1}	7·6	9·2			RM$_{1}$	7·2	5·3
		RM^{2}	8·3	10·0			RM$_{2}$	7·9	6·0
M26564	AW	LDP^{4}	7·1	8·1	M29719–21	AW	RM$_{1}$	7·2	5·1
		LM^{1}	7·7	9·2			RM$_{2}$	8·3	5·6
M25129	AW	LDP^{4}	6·6	8·1			RM$_{3}$	9·8	5·1
		LM^{1}	7·5	8·9	M26906	AW	RM$_{2}$	7·6	5·3
M32142	AW	LP^{4}	6·3	8·0			RM$_{3}$	10·5	5·5
M29716	AW	RM$^{1/2}$	7·7	(8·8)	M29360	AW	RP$_{3}$	5·5	3·7
M29754	AW	RM$^{1/2}$	7·2	8·7	M29715	AW	LP$_{4}$	5·9	4·3
M15140a	AW	RM$^{1/2}$	7·6	–	M32127	AW	RM$_{1/2}$	8·0	5·6
M15139	AW	LM^{3}	7·8	9·8	M15143	AW	RM$_{1/2}$	8·2	5·6
M13762	AW	LM^{3}	7·9	9·2	M29744	AW	LM$_{3}$	10·3	5·4
M15138	AW	LM^{3}	8·4	(8·8)	M15130	AW	RM$_{3}$	10·6	5·5
M15140b	AW	RM$^{1/2/3}$	–	–	M13765	AW	RDP$_{3}$	–	3·6
M29231	AW	LDP^{3}	6·8	6·2	M29645	AW	RDP$_{4}$	7·3	4·6

Hyracotherium vulpiceps

44115	H	RP^{1}	–	–	44115	H	RP$_{1}$	(3·8)	(2·2)
		RP^{2}	5·6	4·3			RP$_{2}$	(6·0)	(2·7)
		RP^{3}	6·1	6·6			RP$_{3}$	(6·3)	(3·8)
		RP^{4}	6·6	7·9			LP$_{4}$	6·6	4·6
		RM^{1}	7·2	9·0			LM$_{1}$	7·4	5·5
		RM^{2}	8·9	10·1			LM$_{2}$	8·5	(6·0)
		LM^{3}	7·5	8·9			RM$_{3}$	(10·5)	6·1
38801	S	LP^{2}	(6·5)	(3·5)					
		RP^{3}	6·4	6·7					
		RP^{4}	7·2	8·3					
		RM^{1}	7·6	9·5					
		RM^{2}	8·2	10·2					
		RM^{3}	7·6	9·5					

Hyracotherium leporinum

M16336	HB	RP^{2}	5·9	3·5	C21361	HB	RP^{2}	6·9	4·1
		LP^{3}	6·8	7·3			LP^{3}	6·7	7·0
		LP^{4}	6·9	8·5			LP^{4}	7·6	8·8
		RM^{1}	7·7	9·7			LM^{1}	8·0	10·3
		RM^{2}	8·6	10·5			LM^{2}	8·5	11·0
		RM^{3}	8·5	10·0			RM^{3}	8·1	10·4

v 1901 *Hyracotherium leporinum* Owen; Depéret : 200–201; pl. 4, fig. 1.
v 1932*b* *Hyracotherium vulpiceps* (Owen); C. F. Cooper : 432–436, text-figs 2D, 3A; pl. 50, figs 1–3; pl. 51, figs 1–3.
v 1952 *Hyracotherium vulpiceps* (Owen), Simpson : 195–206; pl. 37; pl. 38, figs a–d.
v 1952 *Hyracotherium* sp.; Simpson : pl. 40, fig. a.

Holotype. The skull and incomplete skeleton 44115 (also registered on 44115a and M10657–61) still partly embedded in matrix. Simpson (1952 : 196) has described the history of this specimen. A subsequent misfortune has been the disappearance of the almost complete right mandibular ramus which appears to have happened about 1960.

Other material. Damaged cranium with left P^3–M^2 and right P^3–M^3, 38801.

Type horizon and locality. The Harwich Stone Band (= Roman cement bed), lower London Clay of Harwich, Essex.

Range. 38801 is from the Red Crag basement bed, assumed derived from the London Clay.

Emended diagnosis. Medium-sized species of *Hyracotherium* (see Table 1), length of P^2–M^3 41 mm in holotype. Upper molars with very slightly buccally flexed centrocrista and a very faint rib in the mesostylar position, separated from the buccal cingulum. Lower molar metalophids tend to join trigonids equidistant between protoconids and metaconids. M_3 hypoconulid lobe relatively large and with a median main cusp. P^3 with large protoconule; distolingually placed protocone; slightly convex mesiolingual margin and little or no postprotocrista.

Doubtfully referred specimens. There are four other specimens the size of *H. vulpiceps* in the Ipswich Museum from the Red Crag basement bed, presumed to be derived from the London Clay. A palate (IM 1935-64a: E. C. Moor collection) with all the cheek tooth crowns broken off has a P^3 with typical *vulpiceps* outline but, unlike the holotype, a short diastema between P^1 and P^2. A $P\frac{1}{1}$–$P\frac{2}{2}$ diastema was used as a generic character by Kitts (1956). A right maxillary fragment with P^4–M^2 (IM 1935-64b) has upper molar centrocrista with buccal flexure intermediate between the condition in *H. vulpiceps* and that in *H. leporinum*, and P^4 with a slight distal protoconal crest trending distobuccally. A right mandibular fragment with M_{2-3} (IM 1935-64c) has a typically long M_3 hypoconulid lobe. The fourth specimen (IM unnumbered, old collection) is from Falkenham, Suffolk, and is a palate with apparently left and right DP^3–M^2 very abraded. The last two specimens could, on the basis of size, be referred to either *H. vulpiceps* or *H. leporinum*.

Hyracotherium **aff.** ***vulpiceps***

Fig. 2a–c

v 1931 *Hyracotherium* sp.; White : 18, 25.
v 1932*b* *Hyracotherium vulpiceps* (Owen); C. F. Cooper : 433, 437–438; pl. 51, figs 4–5.
v 1952 *Hyracotherium* sp.; Simpson : pl. 40, figs b–d.

Material. See Table 1.

Range. Abbey Wood member of the Blackheath Beds, Abbey Wood, London Borough of Bexley (TQ 4801 7864). Also possibly the Blackheath Beds of Bean, Kent (TQ 590717) based on an upper molar hypoconal fragment (M32179, J. Cooper collection).

Discussion. The Abbey Wood specimens show a very close resemblance to the holotype of *H. vulpiceps* in size and morphology, with the exception of the unique P^3 (M13761). This differs in having a small protoconule, centrolingually placed protocone and straight mesiolingual margin. It thus resembles P^3 of *H. cuniculus* in morphology, but is larger. The combination of very small numbers and different morphology of P^3 in the *H. vulpiceps*/aff. *vulpiceps* complex can be treated in two different ways. We may combine them into one species on the basis of molar identity and assume that the P^{3}s are variable, or we can consider the two assemblages as different on a typological basis, but closely related. The second approach is here preferred as it is less subjective and in particular because the P^3 of *H. cuniculus* and of *H. leporinum* are distinct, contrary to Simpson's statement (1952 : 203).

The constancy of molar characters in *H. vulpiceps* and *H.* aff. *vulpiceps* is supported by the upper molars of eleven individuals, the lower molars of eight individuals and specifically the M$_3$s of five individuals. The left M^3 (M13762, figured C. F. Cooper 1932*b* : pl. 51, fig. 4 lower) shows a straight centrocrista probably as a result of the tapering of the end of the tooth row, which has also resulted in a very lingual metacone.

Hyracotherium leporinum Owen, 1841

Fig. 4a–b

v* 1841 *Hyracotherium leporinum* Owen : 203–208; pl. 2, figs 1–4.
v 1846 *Hyracotherium leporinum* Owen; Owen : 419–423, text-figs 165–167.
v 1932*b* *Hyracotherium leporinum* Owen; C. F. Cooper : 431–446, text-fig. 3B; pl. 49; pl. 50, fig. 4.
v 1952 *Hyracotherium leporinum* Owen; Simpson : 195–206; pl. 39, fig. a.
v 1952 *Hyracotherium* sp.; Simpson : pl. 39, fig. b.

Holotype. Facial part of cranium with alveoli or roots of both canines, both P^{1}s, left P$^{2-3}$, left M^3 and crowns of right P^2–M^3 and left P^4–M^2 (M16336).

Other material. Palate with left and right P^2–M^3 (C21361).

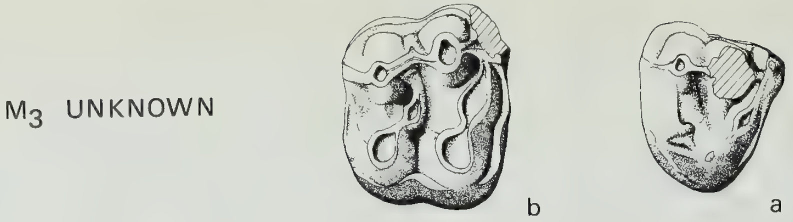
Type horizon and locality. Approximately Division 2 of the London Clay; Studd Hill near Herne Bay, Kent (TR 153677). C21361, labelled 'foreshore Herne Bay', is probably also from here.

Emended diagnosis. Medium-sized species of *Hyracotherium* (see Table 1), length of P^2–M^3 43 mm in holotype. The two available specimens have slightly larger upper premolars and slightly wider upper molars than *H. vulpiceps* (see Fig. 5c–d). Upper molars with strongly buccally flexed centrocrista and weak mesostyle. (Lower molars unknown.) P^3 with small protoconule; centrolingually placed protocone; slightly concave mesiolingual margin; strong postprotocrista present.

Discussion. Of the diagnostic characters only the degree of development of the mesostyle is seen to be slightly variable between the two known upper dentitions; in C21361 it joins the buccal cingulum. In particular the degree of buccal flexing of the centrocrista does not vary and is distinct from *H. vulpiceps* and *H. cuniculus*. The fact that P^3 has a postprotocrista and a slightly concave mesiolingual margin differentiates it from *H. cuniculus* (and from *H. vulpiceps*). Simpson's (1952 : 203) statement that they are very similar is incorrect and his text-fig. 4 is inaccurate. Detail of the postprotocrista in the two specimens is different, it being single and sharp in C21361 and a double structure in the holotype. In the holotype, P^3 and P^4 have a distal protoconal crest (? = postprotocingulum) which fades before reaching the distal cingulum; it is missing on C21361.

Evolutionary trends

Knowing the stratigraphical occurrences of most of the English specimens of *Hyracotherium*, one can see a progression of morphologies through time which shows evolutionary trends, if not the evolution of a single lineage. Figs 1–4 show the changes in P^3, M$^{1/2}$ and M$_3$ in four stages. There is a size increase from stage 1 to 2 and from stage 3a to 4a (the slight width increase of the upper molar from stages 3 to 4 is demonstrated in Fig. 5d, p. 109); the upper molar morphology remains the same from stage 2 to 3; the M$_3$ hypoconulid lobe enlarges, lengthens and becomes more median in position from stage 1 to 2 (and remains unchanged from 2 to 3). At the same time the attachment of the metalophid to the trigonid shifts lingually to a more median position. The actual lengthening of the hypoconulid lobe is demonstrated in Fig. 5a by measuring distances between cusp tips. *H.* aff. *vulpiceps* also shows a relative lengthening of the whole M$_3$ over *H. cuniculus* (Fig. 5b). The specimen of *H.* aff. *vulpiceps* which overlaps greatly with *H. cuniculus*



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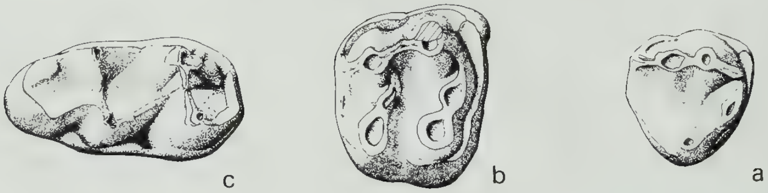

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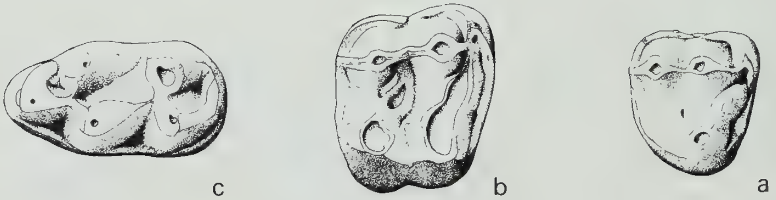

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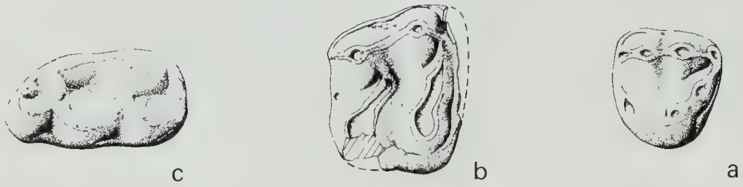

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Fig. 1 *Hyracotherium cuniculus*, from the Suffolk Pebble Beds of Kyson, Suffolk: (a) left P^3 (reversed) (36572); (b) right $M^{1/2}$ (M29709); (c) right M_3 (M29710). All ×3.

Fig. 2 *H.* aff. *vulpiceps*, from the Blackheath Beds of Abbey Wood, London: (a) right P^3 (M13761); (b) left M^1 (reversed) (M25129); (c) right M_3 (M26906). All × 3.

Fig. 3 *H. vulpiceps*, from the Harwich Stone Band, London Clay, Harwich, Essex; holotype (44115): (a) right P^3; (b) composite left and right M^1 (shown as right); (c) right M_3 (drawn from photograph in Cooper, C. F. 1932*b*: pl. 51, fig. 1). All ×3.

Fig. 4 *H. leporinum*, from approximately Division 2, London Clay, Herne Bay, Kent; holotype M16336): (a) right P^3; (b) right M^1. All ×3.

in hypoconulid length (M15130) is nevertheless typical in its overall length/width proportions and appears to have achieved this by relative elongation of the talonid.

Other variable characters such as cingular development and outline shape of upper molars as well as different wear stages (specimens figured chosen as far as possible to show similar wear) make the specimens shown in Figs 1–4 appear more different from one another than their specific diagnoses indicate.

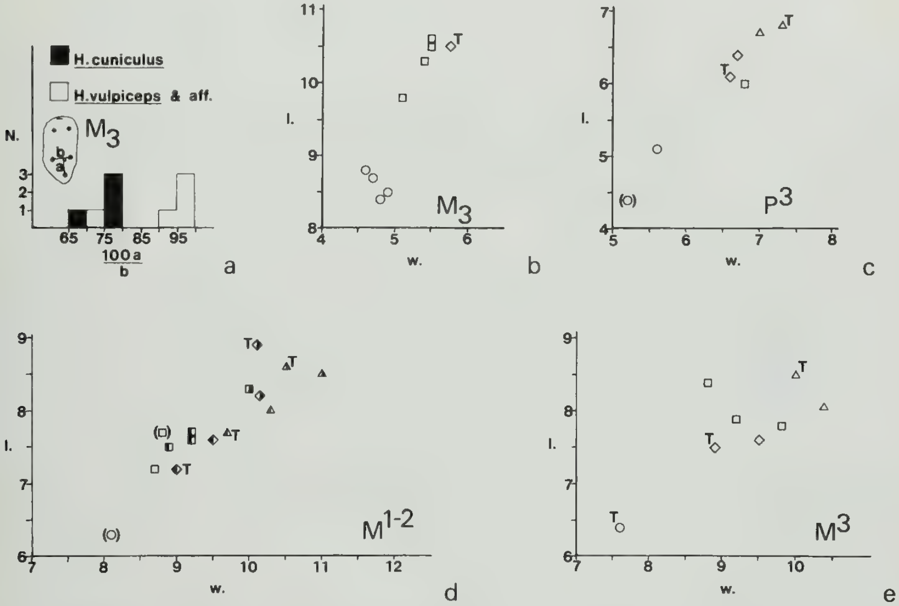

Fig. 5 (a) Histogram of perpendicular distance from hypolophid to hypoconulid (a), as a percentage of hypolophid length (b), in M_3 of *Hyracotherium cuniculus*, *H. vulpiceps* and *H.* aff. *vulpiceps*; (b–e) Scatter diagrams of maximum length (l) and width (w), in mm, of M_3, P^3, M^{1-2} and M^3 respectively. Symbols: *H. cuniculus* (○), *H.* aff. *vulpiceps* (□), *H. vulpiceps* (◇) and *H. leporinum* (△). Symbols in brackets indicate estimates; T indicates a plot of the primary type of a species; in Fig. 5d pre-ultimate molars identified as M^1 or M^2 are indicated by solid left or right half symbol, respectively.

C. F. Cooper (1932*b* : 442–443), unaware that *H. leporinum* occurred above *H. vulpiceps*, considered the latter to be more advanced because its P^3 resembled that of North American late Wasatchian forms such as *H. venticolum* (Cope), which were molarizing their premolars in the direction of *Orohippus*. In England, and probably the rest of Europe, the initial trend of molarization of P^3 by the North American equid method (i.e. by enlargement of the protoconule and distal shift of the protocone) changed to the European palaeothere method (i.e. by addition of a hypocone behind the protocone, as occurred in the molarization of P^4 in both North American and European equoids) in the evolution of *Hyracotherium vulpiceps* to *H. leporinum*. It is possible that it was at this time that the Ypresian transgression finally isolated the North American and European Eocene mammal faunas, whereupon the palaeothere and equid characteristics established themselves.

Potential complications to the evolutionary scheme envisaged here are the *vulpiceps*-sized mandible occurring alongside the M_3 of *H. cuniculus* at Erquelinnes, and a poorly preserved palate (IM, unnumbered), with no data but in preservation identical to those from the Red Crag basement bed, the size of *H. cuniculus*. Nevertheless, the English sequence of species is a useful standard which might be recognized elsewhere in Europe and be used in biostratigraphic correlation. At the moment, however, the limits of the stratigraphical ranges of the various species are too poorly known to erect legitimate biozones for them. Some correlations, however, are suggested below. The occurrences of *H. cuniculus* in the London and Belgian Basins probably mark the time of the initial migration into Europe of the Sparnacian mammal fauna. *Hyracotherium* species from the French Sparnacian, especially the higher parts, are not so easily comparable with the English species, and it is possible that the transgression of the Ypresian sea had by this time isolated the two areas, allowing evolution to occur independently.

Foreign specimens attributed to English species

Savage *et al.* (1965) described *Hyracotherium* from three Paris Basin Sparnacian sites (Pourcy, Mutigny and Avenay). At each the size variation for the few isolated teeth known exceeds that for the English species. In fact the measurements span those of *H. cuniculus* and either *H. vulpiceps* or *H. leporinum*. This fact was recorded by Savage *et al.* (1965) only for the Avenay locality and is reflected in their 'cf. *cuniculum*' (*sic*) identification of the smaller species there. In morphology all these French specimens differ from both *H. cuniculus* and *H. vulpiceps* in the frequent, but not constant, presence of buccally flexed centrocristae and development of mesostyles on the upper molars. Their figures of the upper molars from Pourcy (1965 : text-fig. 3b–d) show slight buccal flexing of the centrocrista. The smaller $M^{1/2}$ (1965 : text-fig. 3b) appears to have a fairly strong mesostyle whilst the larger M^3s (1965 : text-figs 3c–d) appear to have a weaker one somewhat like *H. vulpiceps*. The two M^3s from Mutigny (1965 : text-figs 2f, 2i) appear to have little flexure of the centrocristae and little or no sign of a mesostyle. However, another M^3 (MU12371) and an original (MU12329) and a cast (MU L-218) of two $M^{1/2}$s, which I was able to see when in the Muséum National d'Histoire Naturelle, Paris, have the same centrocristal flexure as *H. leporinum* and a slightly greater mesostyle development. The smaller type from Avenay (referred to by Savage *et al.* (1965 : 11) as *H.* cf. *cuniculum*) differs morphologically from *H. cuniculus*. The $M^{1/2}$ AV4790 (1965 : text-fig. 4c) has a strongly buccally flexed centrocrista and has a mesostyle, the P^4 (1965 : text-fig. 4b) has a weak fold on the distal protocone wall, like the holotype of *H. leporinum*, and the P^3 (1965 : text-fig. 4a) appears to have a well-developed postprotocingulum. The $M^{1/2}$ of the larger type from Avenay (1965 : text-fig. 4f) appears to have a weak centrocristal flexure and no mesostyle. All the M_3s from these three French Sparnacian sites have a relatively long hypoconulid lobe as in *H. vulpiceps* and unlike *H. cuniculus*.

AL5198, the left mandibular fragment with P_4–M_3 from Lemoine's Ageian fauna (a mixture from both the type Sparnacian and the younger Sables à Unios et Térédines), was originally described by Teilhard de Chardin (1922 : 70, text-fig. 33C; pl. 3, fig. 30) as *Propachynolophus* sp. nov. or sp. ind. Savage *et al.* (1965 : 13, text-fig. 4h) referred it to *Hyracotherium* and suggested that it was older than *Propachynolophus* (i.e. Sparnacian) and morphologically intermediate between the two. Its short hypoconulid lobe is reminiscent of *H. cuniculus* but there is no lingual accessory cusp and the animal was closer to *H. vulpiceps* in size. The apparently primitive M_3 suggests that this specimen might be from earlier in the Sparnacian than those from Pourcy, Mutigny and Avenay and it is possible that affinities might lie with the *vulpiceps*-sized mandible from Erquelinnes.

Teilhard de Chardin's (1922 : 52) fig. 26 indicates three teeth of a *Hyracotherium* the size of *H. cuniculus* from the Conglomérat de Meudon, near Paris (at base of the Argile Plastique, considered Sparnacian in age). His discussion, however, indicates an animal the size of *H. leporinum* and the M_3 hypoconulid lobe is indeed longer than that of *H. cuniculus*.

Correlation with continental Europe

Unfortunately, the Paris Basin *Hyracotherium* material is still too poorly known to identify specifically, but the specimens from Mutigny and Avenay appear to be as advanced as the stratigraphically highest English species (*H. leporinum*.). This conforms with Gingerich's (1977 : fig. 8) proposed succession of Sparnacian localities based on the phylogeny of adapid primates. It also suggests, however, that the French Sparnacian localities Mutigny and Avenay are equivalent to the early Ypresian of England. Erquelinnes can be correlated with the Suffolk Pebble

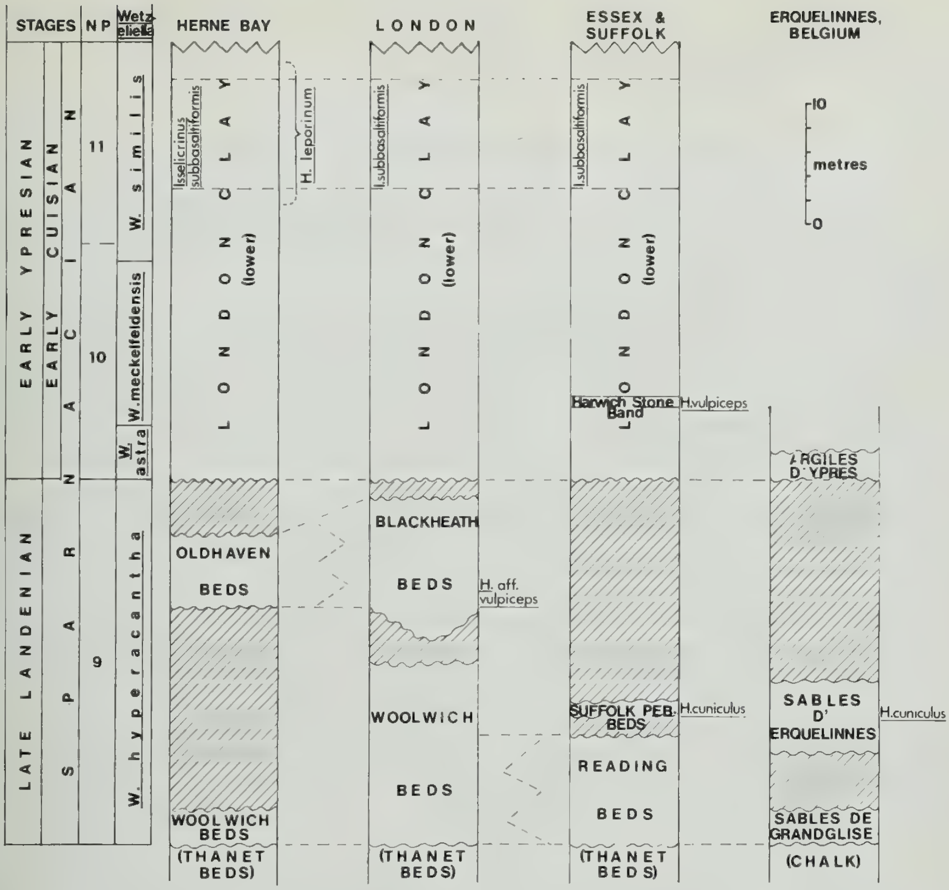
STAGES
NP
Wetzeliella
HERNE BAY
LONDON
ESSEX & SUFFOLK
ERQUELINNES, BELGIUM
EARLY YPRESIAN
EARLY CUISIAN
CUISIAN
SPARNACIAN
LATE LANDENIAN
11
10
9
W. similis
W. meckelfeldensis
W. astra
W. hyperacantha
Isselicrinus subbasaltiformis
I. subbasaltiformis
H. leporinum
LONDON CLAY
LONDON CLAY (lower)
Harwich Stone Band
H. vulpiceps
OLDHAVEN BEDS
BLACKHEATH BEDS
H. aff. vulpiceps
WOOLWICH BEDS
SUFFOLK PEB. BEDS
H. cuniculus
READING BEDS
(THANET BEDS)
ARGILES D'YPRES
SABLES D'ERQUELINNES
SABLES DE GRANDGLISE
(CHALK)
10
metres
0

Fig. 6 Stratigraphic columns showing occurrences of English *Hyracotherium* and correlation with Belgium. The *Wetzeliella* and standard calcareous nannoplankton zones (NP) are after Costa & Downie (1976) and Costa *et al.* (1978). Oblique hatching indicates absence of deposits. The range given for *Isselicrinus subbasaltiformis* follows King (1970).

Beds localities on the common occurrence of *H. cuniculus*, and is here considered to be early Sparnacian. Recently Costa *et al.* (1978) correlated the French Sables de Cuise (type Cuisian) with the English London Clay, already correlated with the Belgian Argiles d'Ypres (type Ypresian) by Costa & Downie (1976), and the French Sparnacian strata with the English Woolwich/Reading Beds and Blackheath/Oldhaven Beds, on the basis of a succession of dinoflagellate zones. This would appear to contradict the evidence from the mammals. However, the Sables de Sinceny and Pourcy ('Upper Sparnacian' of Costa *et al.* 1978), which immediately underlie the Sables de Cuise, have been recognized above an erosion plane in the middle of the type Sparnacian in the region of Épernay (Feugueur 1963 : 288–291). The mammaliferous horizons of Mutigny and Avenay appear to lie above this level (Michaux 1964; Louis 1970 : 58–60) and could therefore both be equivalent to lower levels of the Sables de Cuise; the higher Sables à Unios et Térédines of the Épernay district (classically considered sole Cuisian of the area) would then be equivalent to only the upper part of the type Cuisian. In that case the whole of the Sparnacian of Costa *et al.* (1978), being based on the Soissonnais area, would refer only to the lower part of the type Sparnacian.

According to these correlations, the two species of the plesiadapid primate *Platychoerops*

(*P. daubrei* (Lemoine, 1880) from Pourcy, Mutigny and Avenay and *P. richardsoni* Charlesworth, 1855, from Herne Bay), considered by Gingerich (1976 : text-fig. 19) to have an ancestor–descendant relationship, are approximately contemporaneous.

Comparison with North American material

Few valid comparisons can be made with the North American species of *Hyracotherium* until they are thoroughly revised in a detailed stratigraphic context. Kitts (1956) evidently reduced the number of valid species too drastically without sufficiently good stratigraphic control (see comments by McKenna 1960 : 117–119, Delson 1971 : 355–356, and Guthrie 1967 : 42–45). A few general points can be made. The buccal flexure of the centrocrista and development of the mesostyle on upper molars had hardly begun before the late Wasatchian (e.g. Wind River and Lost Cabin faunas). Moreover, the enlargement of the P^3 protoconule, heralding the premolar molarization of *Orohippus*, had not taken place until this time. English and continental European *Hyracotherium* species appear to have been more precocious in their evolution, as were the later more advanced European palaeotheres over their contemporaneous North American equid relatives.

As in Europe, most of the North American records of *Hyracotherium* are from the early Eocene, but two have been attributed to the Palaeocene (Morris 1968 : 1, Jepsen & Woodburne 1969). The latter record has been discredited by Gingerich (1976 : 51–53) as being in an area of downwarped younger (Wasatchian) early Eocene strata amongst generally older (Palaeocene) strata. The former record is of a small species (*H. seekinsi* Morris, 1968) from the Tepetate Formation of Baja California, Mexico, associated with barylambdid pantodonts and *Esthonyx* sp. The species is based on a few isolated upper molars and appears scarcely more primitive than typical early Wasatchian species, e.g. *H. angustidens* (Cope). Gingerich (1976 : 56–58) correlated the Clarkforkian (the stage immediately preceding the Wasatchian in North America) with the lower Sparnacian of Europe, based on the evolution of plesiadapid primates. There appear to be no records of *Hyracotherium* specifically from the Clarkforkian and so, with the possible exception of *H. seekinsi*, the early Sparnacian *H. cuniculus* is the oldest species of the genus. One of its features which appears to be primitive amongst the European species is the small size of the M_3 hypoconulid lobe. M_3s of this morphology, however, appear to occur randomly in Wasatchian populations (e.g. Savage *et al.* 1965 : text-fig. 5c). This may be another reflection of the generally slower evolution of the North American species compared with the European ones, leading to retention of primitive characters in some individuals. The slightly earlier appearance of *Hyracotherium* in Europe than in the North American Rocky Mountain region might point to an immigration from the east rather than from Central America as postulated by Sloan (1970) and Gingerich (1976 : 86–88).

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References

Boswell, P. G. H. 1916. The stratigraphy and petrology of the Lower Eocene deposits of the north-eastern part of the London Basin. *Q. Jl geol. Soc. Lond.* **71** : 536–591.

Charlesworth, E. 1855. On several new vertebrate fossils. *Rep. Br. Ass. Advmt Sci.*, Liverpool, **24** : 80.

Cooper, C. F. 1932*a*. On some mammalian remains from the Lower Eocene of the London Clay. *Ann. Mag. nat. Hist.*, London, (10) **9** : 458–467, pls 11–12.

—— 1932*b*. The Genus *Hyracotherium*. A revision and description of new specimens found in England. *Phil. Trans. R. Soc.*, London, B **221** : 431–448, pls 49–51.

Cooper, J. 1976. Sections recorded by the Tertiary Research Group at Bramford, 20.11.1971. *Bull. Ipswich geol. Grp* **16** : 11–12.

—— 1977. The palaeontology of the London Clay (Lower Eocene) of the Herne Bay coastal section, Kent, England. *Proc. Geol. Ass.*, London, **88** : 163–178, 1 fig.

Costa, L. I., Denison, C. & Downie, C. 1978. The Paleocene/Eocene boundary in the Anglo-Paris Basin. *J. geol. Soc. Lond.* **135** : 261–264, 2 figs.

—— **& Downie, C.** 1976. The distribution of the dinoflagellate *Wetzeliella* in the Palaeogene of northwestern Europe. *Palaeontology*, London, **19** : 591–614, 6 text-figs, pl. 92.

Davis, A. G. & Elliott, G. F. 1951. The London Clay of coastal Suffolk and Essex. *Geol. Mag.*, London, **88** : 329–338.

Delson, E. 1971. Fossil mammals of the early Wasatchian Powder River local fauna, Eocene of northeast Wyoming. *Bull. Am. Mus. nat. Hist.*, New York, **146** : 305–364, 24 figs.

Depéret, C. 1901. Révision des formes européennes de la famille des Hyracotheridés. *Bull. Soc. géol. Fr.*, Paris, (4) **1** : 199–225, pls 4–5.

Elliott, G. F. 1971. Eocene volcanics in south-east England. *Nature phys. Sci.*, London, **230** : 9.

Feugueur, L. 1963. L'Yprésien du Bassin de Paris. Essai de monographie stratigraphique. *Mém. Serv. Carte géol. dét. Fr.*, Paris. 568 pp, 107 text-figs, 8 pls.

Fitch, F. J., Hooker, P. J., Miller, J. A. & Brereton, N. R. 1978. Glauconite dating of Palaeocene–Eocene rocks from east Kent and the time-scale of Palaeogene volcanism in the North Atlantic region. *J. geol., Soc. Lond.* **135** : 499–512, 14 figs, 2 tabs.

Gamble, H. J. 1979. Observations on some London Clay coastal localities in and around Whitstable, Kent. *Tertiary Res.*, London, **2** (4) : 151–160, 2 text-figs.

George, W. & Vincent, S. 1976. Some river exposures of London Clay in Suffolk and Essex. *Tertiary Res.*, London, **1** : 25–28.

Gervais, P. 1877. Énumération de quelques ossements d'animaux vertébrés recueillis aux environs de Reims par M. Lemoine. *J. Zool., Paris* **6** : 74–79.

Gingerich, P. D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Pap. Paleont. Mus. Paleont. Univ. Mich.*, Ann Arbor, **15**. 140 pp., 42 text-figs, 12 pls.

—— 1977. New species of Eocene primates and the phylogeny of European Adapidae. *Folia primatol.*, Basel, **28** : 60–80, 8 figs.

Guthrie, D. A. 1967. The mammalian fauna of the Lysite member, Wind River Formation (early Eocene) of Wyoming. *Mem. sth. Calif. Acad. Sci.*, Los Angeles, **5** : 1–53.

Hooker, J. J. 1979. Two new condylarths (Mammalia) from the early Eocene of southern England. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **32** (1) : 43–56, 15 figs, 3 tabs.

Jepsen, G. L. & Woodburne, M. O. 1969. Paleocene hyracothere from Polecat Bench Formation, Wyoming. *Science, N.Y.* **164** : 543–547, 1 fig., 2 tabs.

King, C. 1970. The biostratigraphy of the London Clay in the London district. *Tertiary Times*, Bromley, **1** : 13–15.

Kitts, D. B. 1956. American *Hyracotherium* (Perissodactyla, Equidae). *Bull. Am. Mus. nat. Hist.*, New York, **110** : 1–60, 7 pls, 10 figs.

Kühne, W. G. 1969. A multituberculate from the Eocene of the London Basin. *Proc. geol. Soc. Lond.* **1658** : 199–202, 1 fig.

Lemoine, V. 1880. Sur les ossements des terrains tertiaires inférieurs des environs de Reims. *C. r. Ass. fr. Avanc. Sci.*, Paris, **8** : 585–594.

—— 1887. Sur le genre *Plesiadapis*, mammifère fossile de l'Éocène inférieur des environs de Reims. *C. r. hebd. Séanc. Acad. Sci. Paris* **1887** : 190–193.

Louis, P. 1970. Note préliminaire sur un gisement de mammifères de l'Éocène inférieur situé route de Broyes à Sézanne (Marne). *Annls Univ. ARERS*, Reims, **8** : 48–62.

Lydekker, R. 1886. *Catalogue of the fossil Mammalia in the British Museum* (*Natural History*), **3**. xvi + 186 pp., 30 figs. British Museum (Natural History), London.

McKenna, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile Fauna, Eocene of northwest Colorado. *Univ. Calif. Publs geol. Sci.*, Berkeley, **37** (1). 130 pp., 64 text-figs.

Marsh, O. C. 1876. Notice of new Tertiary mammals. *Am. J. Sci.*, New Haven, **12** : 401–404.

Matthews, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, London, **16** (4) : 713–719.

Michaux, J. 1964. Age des Sables à Unios et Térédines (Éocène inférieur) d'Avenay (Marne) et leurs relations avec les Sables du même nom des gisements classiques d'Épernay. *C. r. somm. Séanc. Soc. géol. Fr.*, Paris, **1964** (3) : 103.

Morris, W. J. 1968. A new early Tertiary perissodactyl, *Hyracotherium seekinsi*, from Baja California. *Contr. Sci. Los Angeles* **151** : 1–11, 4 figs, 1 pl.

Owen, R. 1839. Description of the Fossil mentioned in the preceding letter. *Mag. nat. Hist.*, London, NS **3** : 446–448, text-fig. 58A–C.

—— 1841. Description of the Fossil Remains of a mammal (*Hyracotherium leporinum*) and of a bird (*Lithornis vulturinus*) from the London Clay. *Trans. geol. Soc. Lond.* (2) **6** (1) : 203–208, pl. 21.

—— 1842. Description of some Molar Teeth from the Eocene Sand at Kyson in Suffolk, indicative of a new species of *Hyracotherium* (*Hyr. Cuniculus*). *Ann. Mag. nat. Hist.*, London, **8** : 1–2, text-figs 1–5.

—— 1846. *A History of British Fossil Mammals and Birds.* 560 pp., 237 text-figs. London.

—— 1858. Description of a small Lophiodont Mammal (*Pliolophus vulpiceps* Owen) from the London Clay near Harwich. *Q. Jl geol. Soc. Lond.* **14** : 54–71, pls 2–4.

—— 1865. On a new genus (*Miolophus*) of mammal from the London Clay. *Geol. Mag.*, London, (1) **2** : 339–341, pl. 10.

Prestwich, J. 1850. On the structure of the strata between the London Clay and the Chalk in the London and Hampshire Tertiary Systems. *Q. Jl geol. Soc. Lond.* **6** : 252–281.

Quinet, G. E. 1969. Apport de l'étude de la faune mammalienne de Dormaal à la stratigraphie générale du Paléocène supérieur européen et à la théorie synthétique de la molaire mammalienne. *Mém. Inst. r. Sci. nat. Belg.*, Brussels, **162.** 188 pp., 7 pls.

—— **& Verlinden, W.** 1970. Sur l'*Hyracotherium* d'Erquelinnes (Jeumont). *Bull. Inst. r. Sci. nat. Belg.*, Brussels, **46** (34) : 1–10, 3 pls.

Richardson, W. 1841. Observations on the locality of the *Hyracotherium. Trans. geol. Soc. Lond.* (2) **6** (1) : 211–214.

Russell, D. E., Louis, P. & Savage, D. E. 1967. Primates of the French early Eocene. *Univ. Calif. Publs geol. Sci.*, Berkeley, **73.** 46 pp., 14 text-figs.

Rutot, A. 1881. Sur la position stratigraphique des restes de mammifères recueillis dans les couches de l'Éocène inférieur de Belgique. *Bull. Acad. r. Belg.*, Brussels, (3) **1** : 506–547, 3 pls.

Savage, D. E., Russell, D. E. & Louis, P. 1965. European Eocene Equidae (Perissodactyla). *Univ. Calif. Publs geol. Sci.*, Berkeley, **56.** 94 pp., 1 pl., 42 text-figs.

Simpson, G. G. 1952. Notes on British Hyracotheres. *J. Linn. Soc.*, London, (Zool.) **42** : 195–206, 4 figs.

Sloan, R. E. 1970. Cretaceous and Paleocene terrestrial communities of Western North America. *In* van Valen, L. (ed.), *Evolution of Communities* : 427–453, 8 figs. Lawrence, Kansas (*Proc. N. Am. paleont. Conv.* **E**).

Teilhard de Chardin, P. 1922. Les mammifères de l'Éocène inférieur français et leurs gisements [cont'd.] *Annls Paléont.*, Paris, **11** : 1–108, text-figs 3–42, pls 1–8.

—— 1927. Les mammifères de l'Éocène inférieur de la Belgique. *Mém. Mus. r. Hist. nat. Belg.*, Brussels, **36.** 33 pp., 6 pls, 29 text-figs.

White, E. I. 1931. *The vertebrate faunas of the English Eocene.* **1.** 123 pp., 1 pl., 162 text-figs, 4 tabs. London, British Museum (Natural History).

Wood, S. V. 1839. Letter from S. V. Wood Esq., late curator to the Geological Society, announcing the discovery of Fossil Quadrumanous remains, near Woodbridge, Suffolk. *Mag. nat. Hist.*, London, NS **3** : 444–445, text-fig. 57.

Wortman, J. L. 1896. Species of *Hyracotherium* and allied perissodactyls from the Wahsatch and Wind River beds of North America. *Bull. Am. Mus. nat. Hist.*, New York, **8** : 81–110.

Wrigley, A. 1924. Faunal divisions of the London Clay illustrated by some exposures near London. *Proc. Geol. Ass.*, London, **35** : 245–259.

Salenia trisuranalis sp. nov. (Echinoidea) from the Eocene (London Clay) of Essex, and notes on its phylogeny

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Synopsis

The new species *Salenia trisuranalis*, with three suranal plates, is described from the English Eocene, and its phylogenetic position with respect to other echinoids discussed in the light of Hennigian methodology. The presence of suranal plates tessellated into the apical disc is seen as likely to be a synapomorphy with irregular echinoids, and suggests they are probably the sister group to the Salenioida.

Introduction

Salenioids, after their great expansion in the Cretaceous, are uncommon subsequently, and in the Eocene are very rare indeed. *Salenia trisuranalis* sp. nov. is the first record of a *Salenia* from the British Cainozoic. Two continental species from the Eocene – *S. pellati* from La Gourèpe near Biarritz, and *S. garciae* from Callosa, Alicante, have certain similarities, but neither has more than one suranal plate.

Salenia trisuranalis is now described, and an attempt is made to assign it to its phylogenetic position with respect to other echinoids.

Systematic description

Superorder **ECHINACEA** Claus, 1876
Order **SALENIOIDA** Delage & Hérouard, 1903
Family **SALENIIDAE** L. Agassiz, 1838
Subfamily **SALENIINAE** L. Agassiz, 1838

Genus ***SALENIA*** Gray, 1835
Salenia trisuranalis sp. nov.
Figs 1–4

DIAGNOSIS. The species is characterized by having three suranal plates.

MATERIAL (Figs 1, 2). The unique holotype is well preserved, slightly crushed and flattened in the ambital plane. One spine is preserved, an interambulacral, on the oral surface. The specimen is in the Palaeontology Department of the British Museum (Natural History), number E76505. It is from the London Clay (Lower Eocene) of Walton-on-the-Naze, Essex, England and was collected by Mr William George.

SHAPE. The test is small, circular in outline at the ambitus, with a maximum diameter of 8·25 mm, minimum 7·5 mm; the exact measurement is uncertain because of the damaged state of the test. The oral surface is flat; the apical surface is irregular owing to plate displacement.

APICAL SYSTEM. This is dicyclic with three suranal plates. (Notation follows Lovén 1874).

Ocular Plates. The inner sutures are rounded, and the outer suture is a single arc. The ornament consists of fine ridges arranged approximately perpendicular to each inner suture. The centre of

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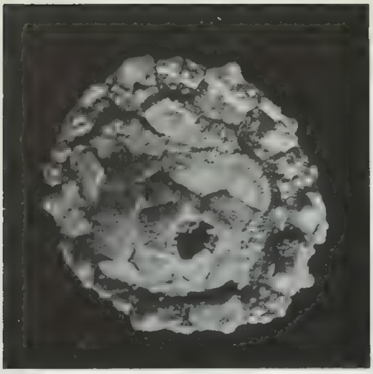

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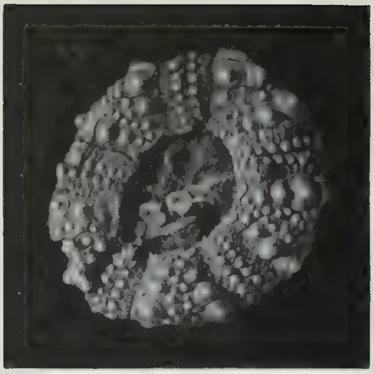

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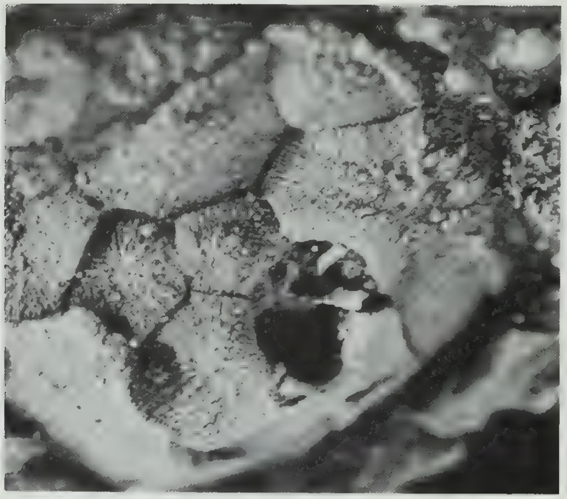

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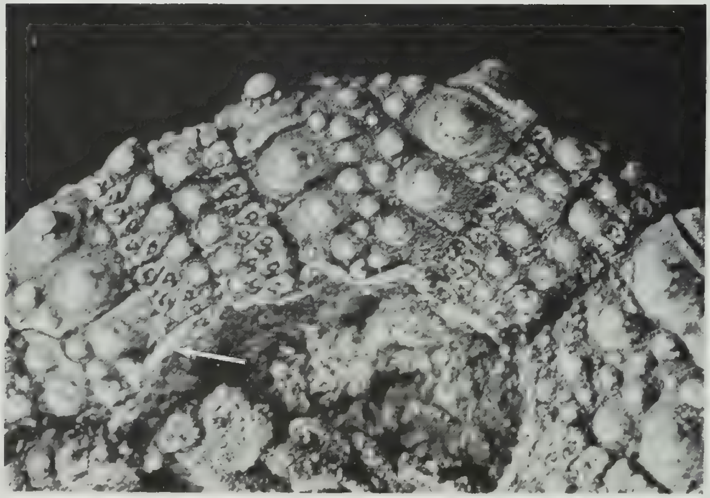

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Figs 1–4 *Salenia trisuranalis* sp. nov. **Holotype**. Fig. 1, adapical view, ×5. Fig. 2, adoral view, ×5. Fig. 3, close-up of periproct to show the three suranal plates, ×15. Ornament of fine ridges and granules, found over the whole of the apical system, can be seen on the suranal plates. Fig. 4, close-up of ambulacra II and III and interambulacrum 2, ×13. A small spine is visible, attached to interambulacrum 1, innermost margin (arrowed).

each ocular plate has granular ornament, and the outer edge has a knobbly ridge the whole of its length. Each ocular plate has a slightly raised, broad v-shaped notch for the ocular tentacle, in the centre of the ridge.

Genital Plates. Genital plate 1 is polygonal, with a shallow notch which is ornamented by fine ridges and which forms part of the slightly raised rim around the periproct. The plate ornament consists of fine ridges approximately perpendicular to the margins, a granular central ornament and a knobbly ridge, concave to the outer margin and in continuation with the ridges on ocular plates I and II. External to this ridge more granules ornament the surface.

Genital plate 2 is octagonal, with ornament similar to that of genital plate 1, comprising fine ridges perpendicular to the inner five margins; the central part of the plate is divided into an inner portion with an irregular surface, and radiating from this an outer portion with granular ornament. There is no continuation of the knobbly ridge from adjacent oculars. However, the granular ornament ceases where the ridges of the oculars meet the plate margin. Connecting the outer two sutures is a convex strip of unornamented plate. There is no external evidence of the madreporic pores.

Genital plate 3 is heptagonal, with a similar ornament of fine ridges around the inner five margins. The centre has granular ornament which radiates towards the outer two sutures and, as in genital plate 2, has an unornamented arcuate strip.

Genital plate 4 is displaced and therefore the boundary is not wholly visible. The plate is polygonal, with ornament like that of genital plates 2 and 3.

Genital plate 5 is polygonal but the outer margin is not visible. A deep notch forms part of the rim around the periproct. Ornament is of fine ridges along the margins as on the other genital plates, but the centre has granular ornament and a knobbly ridge meeting the adjacent oculars, as on genital plate 1.

Suranal Plates (Fig. 3; for discussion see Duncan & Sladen 1887). There are three suranal plates, two along the axis connecting ambulacrum III with interambulacrum 5, and one to the right of this axis, towards ocular plate II. One suranal plate, towards genital plate 5, is larger than the other two and has five straight sides with ornament of fine ridges, and one curved side that makes up part of the periproct rim. The centre of this suranal plate has fine granular ornament, with fine ridges converging into this ornament. The second suranal plate has four straight sides and one smoothly curved side which, again, forms part of the rim of the periproct. The ornament is similar to that of the larger suranal plate. The third suranal plate is partly obscured by genital plate 4 which has overridden it in crushing; however it is pentagonal, with ornament like that of the other two suranal plates.

Periproct. This is bounded by genital plates 1 and 5, and by two suranal plates. The outline is smooth and kidney-shaped, and lies right of the anteroposterior axis (ambulacrum III – interambulacrum 5) and between ocular plate I and two of the suranal plates. The ornament consists of short fine ridges perpendicular to the edges.

Notes on the ornament. The whole of the apical system is ornamented by granules and fine ridges, and in addition by larger knobbly ridges. The fine ridges are continuous from one plate to those adjacent. The genital plates are not perforated by genital pores, suggesting that the individual may be immature.

AMBULACRA (Fig. 4). These are straight and wide. At the peristome they are the same width as the interambulacrals. At the ambitus they are half as wide as the interambulacrals, while at the apical system they are slightly less than half as wide as the interambulacrals.

The plating is difficult to determine except where displaced along the plate boundaries by crushing, but it appears to be bigeminate, with pore pairs oblique.

The pore pairs are surrounded by a smooth deep wall, higher on the aboral side and incomplete on the adoral side. The pores are separated by a single granule situated only slightly towards the adradial suture.

There are 18 primary ambulacral tubercles in each ambulacrum. Each tubercle is large, smooth and in contact with the perradial suture and also close to the pore pairs, with each tubercle covering at least half the width of the plate. The smallest primary tubercles are the first two or three pairs nearest to the peristome, and the largest are developed at the ambitus. Small inner tubercles are also present.

INTERAMBULACRA (Fig. 4). These widen rapidly from the peristome. The interambulacrals are twice as wide at the ambitus as they are at the peristome, and have ten primary tubercles, with one on each plate. The tubercles are situated close to the adradial sutures. In the interradial position there are numerous smaller tubercles, two per larger primary tubercle. Very occasional granules are also present. Plate boundaries are difficult to determine except where dislocated.

The primary tubercles are non-perforate, and have 8–11 crenulations according to size. All smaller tubercles are non-crenulate.

The bosses of the primary tubercles are convex, rising from a rounded basal terrace. The mamelons have slightly undercut necks. Smaller tubercles have convex bosses arising from shallow, rounded basal terraces, and have very short, slightly undercut necks.

PERISTOME. This is large, round, about 4 mm in diameter, and is slightly distorted (*post mortem*). Remains of the raised rim of the gill slits can be seen on ambulacra III and IV and on interambulacra 1, 2, 4 and 5, the others having been broken away.

SPINE (Fig. 4). One spine is present on interambulacrum 1, near the peristome. It is about 0·9 mm long and is not in life position. It is straight, flattened and ornamented by rows of thorns. It tapers proximally into a short neck and ends in a slightly expanded base.

COMPARISON with other species. The specimen, which was first mentioned by George & Vincent (1977), was initially identified as *Salenia* cf. *pellati* on the basis of Cotteau's figures (1860, 1892). However, closer examination reveals some differences, the chief of which is the presence of three suranal plates in *S. trisuranalis* and only one in *S. pellati*. The ornament on the ocular plates of *S. trisuranalis* is like that on the genital plates, but on *S. pellati* it is different – the ribbing is coarser on the ocular plates, and these are perforate. The apical disc covers about the same area in both species. The peristome appears larger in *S. pellati* where it is about the same diameter as the apical disc, whereas in *S. trisuranalis* it is smaller than the apical disc.

Ambulacra are similar to those of *S. pellati* in width, size and numbers of primary tubercles. In *S. pellati* pore pairs open '. . . at the base of a small granular swelling . . .', while in *S. trisuranalis* they are surrounded by a deep wall. Interambulacra are different from those of *S. pellati* in that *S. trisuranalis* has more primary tubercles, although these are similar to that species in structure and numbers of crenulations. *S. garciae* Cotteau (1890) differs slightly in detail, although the type specimen was incomplete, so that the apical disc was not described. The interambulacra of *S. garciae* have many more granules around the primary tubercles and the ambulacra are longer, narrower and have more tubercles. The pore pairs of *S. garciae* appear to have little ornament around them.

Discussion

The Salenioids are divided in the Treatise of Invertebrate Paleontology (Fell & Pawson 1966) into two families – the Acrosaleniidae and the Saleniidae. The Saleniidae are in turn divided into the Saleniinae and the Hyposaleniinae. In the light of Hennigian methodology (Hennig 1966, 1969) it is interesting to consider the phylogenetic relationships of these and other groups.

All known Salenioids are distinguished from other echinoids, except primitive irregular forms, by having one or more suranal plates tessellated into a large apical disc. Many echinoids have an obvious suranal plate in the imago, but usually this later becomes lost amongst the other periproctal plates (see, for example, Gordon 1926, on *Psammechinus miliaris*). The presence of suranal plates tessellated into the apical disc is an advanced character with respect to other echinoids and could be a synapomorphy of Salenioids and irregular echinoids. It suggests that Salenioids may be the sister group of the irregular echinoids (see Jesionek-Szymańska 1968). Its retention in the Salenioids is a paedomorphic character, but its tessellation into the apical disc is not paedomorphic.

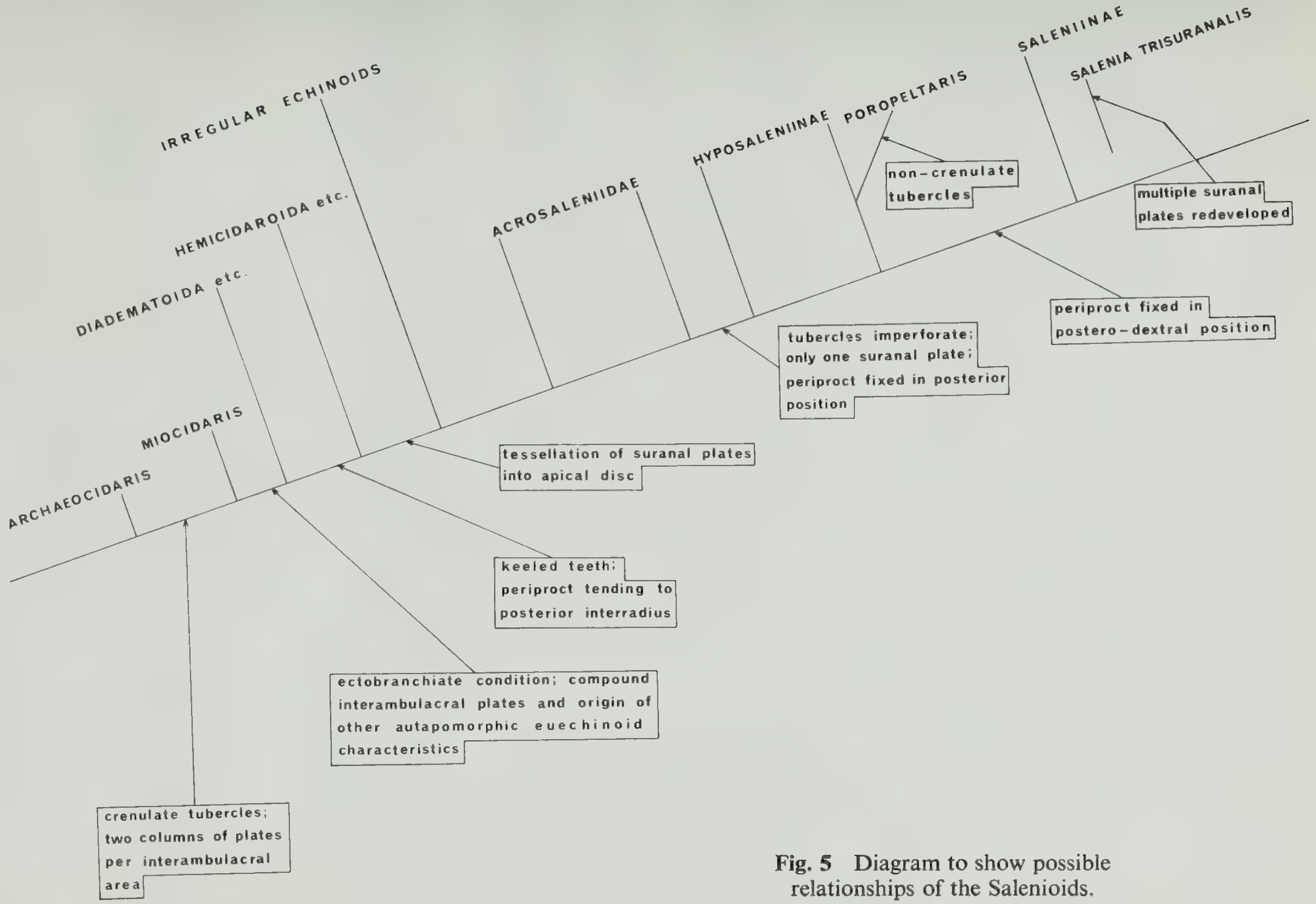
IRREGULAR ECHINOIDS
HEMICIDAROIDA etc.
DIADEMATOIDA etc.
MIOCIDARIS
ARCHAEOCIDARIS
ACROSALENIIDAE
HYPOSALENIINAE
POROPELTARIS
SALENIINAE
SALENIA TRISURANALIS
non-crenulate tubercles
multiple suranal plates redeveloped
periproct fixed in postero-dextral position
tubercles imperforate; only one suranal plate; periproct fixed in posterior position
tessellation of suranal plates into apical disc
keeled teeth; periproct tending to posterior interradius
ectobranchiate condition; compound interambulacral plates and origin of other autapomorphic euechinoid characteristics
crenulate tubercles; two columns of plates per interambulacral area

Fig. 5 Diagram to show possible relationships of the Salenioids.

The Acrosaleniidae probably include the most primitive members of the Salenioids. The reasons for this belief are three. They are geologically early compared with other Salenioids, they have perforate, crenulate primary tubercles, like those of other primitive Euechinoids and *Miocidaris* and they have a tendency, not expressed in all forms, for the periproct to be posterior in position (toward genital plate 5). These characters are likely to be primitive, by an outgroup comparison with irregular echinoids. The difficulty with the comparison is that the position of the periproct is not fixed in genera of the Acrosaleniidae.

However, the tessellation of more than one suranal plate into the apical disc in the Acrosaleniidae is likely to be an advanced condition with respect to many non-Salenioid echinoids, on the grounds of geological age and correlation with the three characters listed above. Salenioids outside the Acrosaleniidae have only one suranal plate tessellated into the apical disc, with the single exception of *S. trisuranalis*.

The Hyposaleniinae are more advanced than the Acrosaleniidae in three respects. The primary tubercles are imperforate, the periproct is fixed in a posterior position, towards genital plate 5, and only one suranal plate is tessellated into the apical disc. The last two characters are likely to be advanced with respect to the acrosaleniid condition on the grounds of geological age. Within the Hyposaleniinae the genus *Poropeltaris* is strikingly characterized by the advanced feature of smooth primary interambulacral tubercles.

The Saleniinae are more advanced than the Hyposaleniinae in having the periproct fixed in a posterodextral position, i.e. near to ocular plate I.

The likely phylogenetic relationships within the Saleniids and some related groups are as shown in Fig. 5. If this figure is correct then the Acrosaleniidae and Hyposaleniinae are groups different in nature from the Saleniinae. In Hennigian terms they are paraphyletic, in that they exclude forms descended from members of the group. Indeed, the Acrosaleniidae and the Hyposaleniinae would be parts of the Hennigian stem-group of the Saleniinae – they would be intermediate categories, *Zwischenkategorien* in the terminology of Hennig (1969).

As regards the multiple suranals of *S. trisuranalis*, two possibilities need to be considered. The first is that the condition is homologous with the similar state of the Acrosaleniidae. This would imply that development of imperforate tubercles and the fixation of the periproct in a posterodextral position had happened twice. It would also imply that Salenioids with more than one suranal plate should exist beyond the Upper Cretaceous. Despite an extensive geological record up to the Upper Cretaceous, Salenioids with more than one suranal plate have not been observed in post-Cretaceous rocks, with the exception of *S. trisuranalis*.

The second possibility is that the multiple suranal plates of *S. trisuranalis* are a convergence with *Acrosalenia*, aping the primitive condition. This seems more likely than the first possibility. Indeed, the condition in *S. trisuranalis* may even prove to be an individual variation. Nevertheless, the rarity of the species has prompted us to describe it, in the hope that this note will encourage the search for further specimens.

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References

Cotteau, G. H. 1860. Échinides nouveaux ou peu connus. *Revue Mag. Zool.*, Paris, (2) **12** : 212–224, pls 12, 13.

—— 1889–94. Terrains Tertiaires, Éocène, Échinides, **2.** 789 pp., pls 201–384. *Paléont. fr.*, Paris (1, *Animaux Invertébrés*).

—— 1890–91. Échinides Éocènes de la Province d'Alicante. *Mém. Soc. géol. Fr.*, Paris, (3) **5** : 1–107, pls 22–37.

Duncan, P. M. & Sladen, W. P. 1887. On some points in the morphology and classification of the Saleniidae, Agassiz. *Ann. Mag. nat. Hist.*, London, (5) **19** : 117–136.

Fell, H. B. & Pawson, D. L. 1966. Echinodermata. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **U** : U211–U640. Kansas.

George, W. & Vincent, S. 1977. Report of field meeting to Walton-on-the-Naze and Wrabness, Essex, 2.10.1976 with notes on the London Clay of Walton. *Tertiary Res.*, West Wickham, **1** (3) : 83–90.

Gordon, I. 1926. The development of the calcareous test of *Echinus miliaris*. *Phil. Trans. R. Soc.*, London, B **214** : 259–312.

Hennig, W. 1966. *Phylogenetic Systematics*. 263 pp. Urbana, Ill.

—— 1969. *Die Stammesgeschichte der Insekten*. 436 pp. Frankfurt a.M.

Jesionek-Szymańska, W. 1968. Irregular echinoids – an insufficiently known group. *Lethaia*, Oslo, **1** (1) : 50–62.

Lovén, S. 1874. Études sur les Échinoidées. *K. svenska VetenskAkad. Handl.*, Uppsala & Stockholm, **11** : 1–191, 53 pls.

Tertiary and Cretaceous brachiopods from Seymour, Cockburn and James Ross Islands, Antarctica

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Synopsis

The systematics of the brachiopod fauna described by Buckman (1910) from the Lower Tertiary of Seymour and Cockburn Islands is revised. New species *Notosaria seymourensis*, *Terebratulina buckmani*, *Terebratella crofti* and *Liothyrella anderssoni* are described, as is the dallinoid '*Laqueus*' *cockburnensis*, broadly assigned to that genus. Present views on the stratigraphical position and latest age estimates for the Lower Tertiary beds of Seymour Island are briefly discussed.

Descriptions of new genera and species *Protegulorhynchia meridionalis* (Hemithyrididae) and *Rossithyris humpensis* (Laqueidae), from the Upper Cretaceous, Campanian of James Ross Island, are given for the first time.

Introduction

Andersson (1906) recognized two distinct lithologies within the Tertiary sequence on Seymour Island. One of these he described as a calcareous sandstone with tuff fragments, located chiefly in the Cross Valley area, while the remaining deposits were said to be friable sandstones with conglomerate intercalations. Plant remains were abundant in the calcareous sandstones and numerous invertebrate fossils, mainly brachiopods and molluscs, occurred in the more friable beds. The term Seymour Island Series was applied to the entire sequence.

Adie (1958 : 9) pointed out the existence of a major unconformity between the Tertiary and Cretaceous deposits which occur south-west from Cross Valley and also crop out at the most northerly point, Cape Wiman. Since this work, very few stratigraphical observations have been made on the island, but in 1974–75 an expedition, conducted by members of the Institute of Polar Studies at Ohio University, led to a publication by Elliot & Trautman (1979) who revised the Tertiary deposits and proposed the following formations.

a. Cross Valley Formation, for the sequence of non-marine sandstone and plant-bearing fine sandstone which crops out in Cross Valley and is regarded as of Palaeocene age.

b. La Meseta Formation, for the unconsolidated marine sands exposed on the flanks and to the north of the mesa situated on the north-eastern part of the island. The suggested age of the beds was late Eocene to early Oligocene, a view expressed also by Zinsmeister (1977) on the basis of faunal and floral evidence.

In the same paper, Zinsmeister (1977) points out that Wilkens' (1911) correlation of the 'Seymour Island Series' with the Patagonian Formation, though correct in chronological position, was wrongly dated as Oligocene–Miocene and should be regarded as older. He quoted the work of Comacho (1974; Comacho & Fernandez 1955), recording several species of *Venericardia planicosta* group bivalves from the lower part of the Patagonian Formation in central Patagonia. The presence of this cosmopolitan bivalve suggested to Comacho that the lower two-thirds of the formation was of Eocene age and that only the uppermost marine unit was of Oligocene age. Thus, according to Zinsmeister, the beds of the Seymour Island Series can be assigned an Eocene to Early Oligocene age with perhaps some of the Lower and Middle Eocene missing.

Other opinions vary with those of Cranwell (1959), who regarded the same deposits as Palaeocene, on the evidence of plant microfossils, and Simpson (1971), who assigned a late Eocene to

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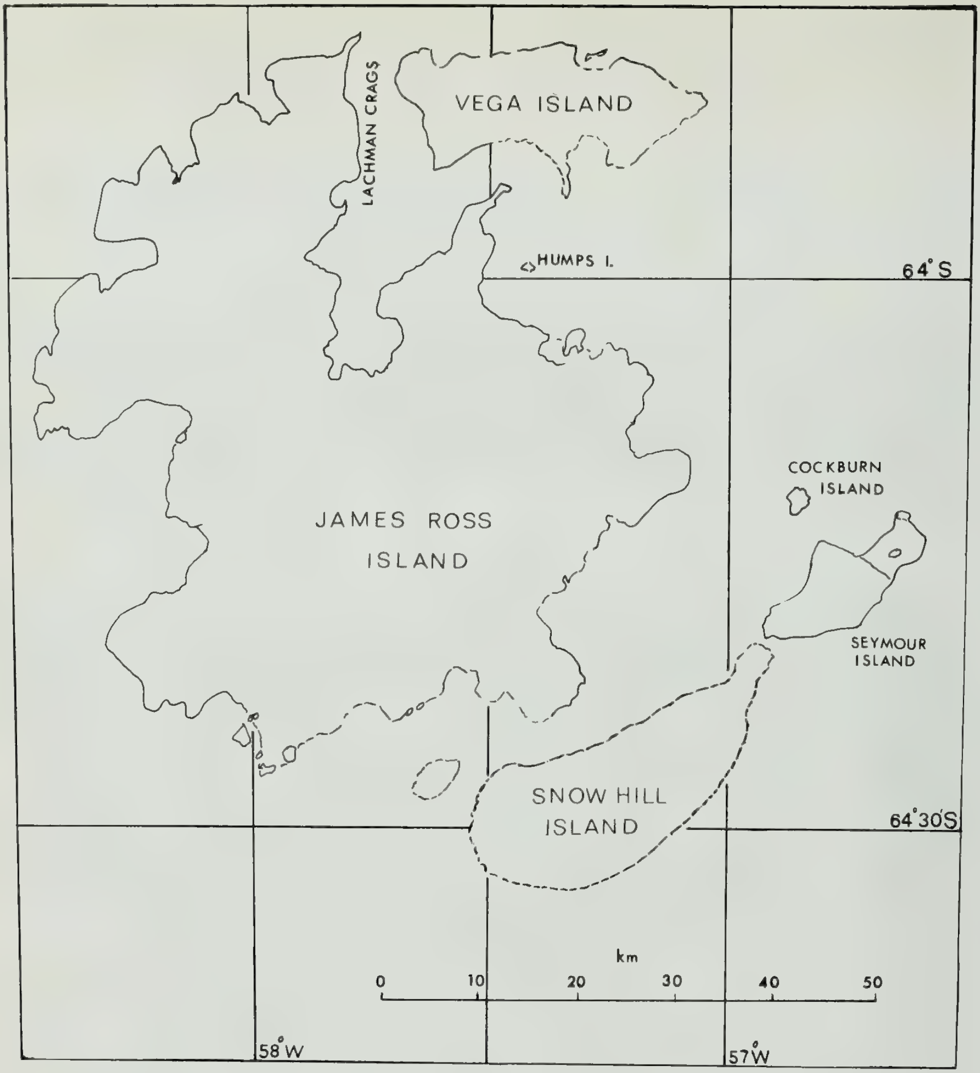
LACHMAN CRAGS
VEGA ISLAND
HUMPS I.
64°S
JAMES ROSS ISLAND
COCKBURN ISLAND
SEYMOUR ISLAND
SNOW HILL ISLAND
64°30'S
km
0
10
20
30
40
50
58°W
57°W

Fig. 1 Sketch map showing the relative positions of Seymour, Cockburn and James Ross Islands.

possibly early Oligocene age from the evidence of fossil penguin bones. Zinsmeister points out that Cranwell's data apply to the lower 110 m of the Seymour Island Series and that the upper 420 m contains a molluscan fauna which suggests an early Oligocene age.

Buckman (1910) interpreted the age of the beds on Seymour Island as Pliocene–Miocene on the evidence of a collection made by the Swedish explorer Dr J. Gunnar Andersson (1901–03) from one locality which Andersson called Loc. 11, and compared the brachiopods to Patagonian species. Those specimens from two further localities, Locs 12 and 13 on Cockburn Island, were ascribed a Miocene–Oligocene and a Pleistocene age, respectively, and compared to Australasian and South American species.

The brachiopods described here are from two collections, one made in 1947 by the late W. N. Croft from Seymour and Cockburn Islands, with additional Cretaceous material from James

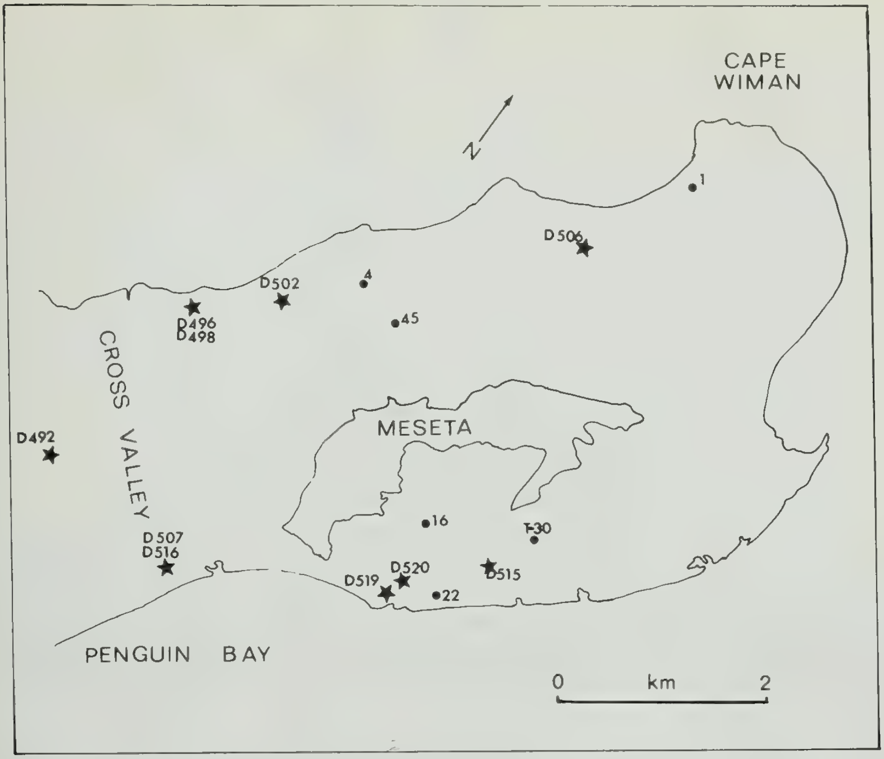

Fig. 2 Outline map of the northern sector of Seymour Island, showing the stations from which brachiopods have been collected. Prefix D indicates W. N. Croft's localities. Plain numerals are IPS localities.

Ross Island, and the other from a more recent visit to Seymour Island by D. H. Elliot and T. A. Trautman in 1974–75.

Unless otherwise stated, all material cited is preserved in the fossil brachiopod collections of the Department of Palaeontology, British Museum (Natural History); registered numbers are prefixed BB.

IPS refers to the Institute of Polar Studies, Ohio State University, U.S.A.

Using simple age and lithological terms, Croft divided the formations on Cockburn Island into the following groups.

1. Intrusive rocks of uncertain age
2. Pecten Conglomerate of Pliocene–Pleistocene age
3. Ross Island Formation
4. Tertiary beds with a brachiopod fauna
5. Cretaceous beds with ammonites

Croft stated in his original unpublished report (1947 : 3) that Andersson's locs 12 and 13 were visited and their positions corrected to points further north than those given on Anderson's sketch map, and on the west side of the island. It is clear from his notes that Croft was somewhat disorientated, since Andersson's sketch (1906 : 6) shows the localities situated on the south-eastern part of the island. Furthermore, Andersson (1906 : 41, fig. 3) gives a section through the beds on the 'East side of Cockburn Island at locality 12'.

Both the brachiopod fauna from Seymour Island and the fauna from the Tertiary beds of Cockburn Island are almost identical in constitution to those described by Buckman (1910),

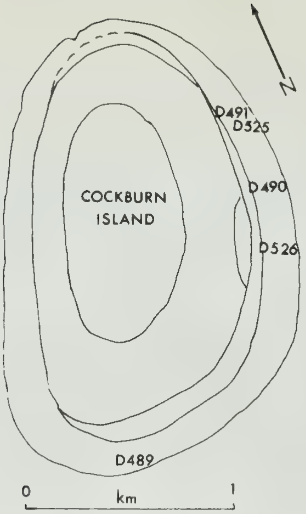

Fig. 3 Sketch map of Cockburn Island showing W. N. Croft localities.

which were based on material collected by Drs O. Nodenskjöld and J. Gunnar Andersson during the Swedish Antarctic Expedition of 1902–03. The present paper is, therefore, very largely a revision of Buckman's work, bringing the systematic and taxonomic aspects up to date.

Systematic descriptions

Superfamily **LINGULACEA** Menke, 1828

Family **LINGULIDAE** Menke, 1828

Genus ***LINGULA*** Bruguière, 1797

Lingula antarctica S. S. Buckman

Fig. 10

1910 *Lingula antarctica* S. S. Buckman : 9; pl. 1, fig. 7.

Buckman described this species as an elongate, parallel-sided shell with rather flat valves, having growth-lines forming an oblong pattern throughout its life history. He figured a rather poorly preserved and incomplete specimen which he felt resembled *Glottidia palmeri* Davidson, but without any of the characteristic median ridges within the dorsal valve.

The specimen figured here, Fig. 10, is just 30 mm in length, about 5 mm longer than Buckman's figured specimen. It was collected by members of the expedition of 1974–75 mounted by the IPS (see p. 123) and comes from their loc. 16, approximately 1 km north of the eastern headland of Penguin Bay, Seymour Island. It is preserved in a highly glauconitic sandstone of Lower Tertiary age.

Buckman's specimen, which was collected from a point further eastward and nearer the coast, is from Loc. 11 of Nordenskjöld & Andersson, 1902–03, and mentioned by Buckman (1910 : 3) as having abundant *Bouchardia* specimens and '. . . crowded with examples of a small *Cerithium*', recently reidentified by Mr R. J. Cleevely, British Museum (Natural History), as *Turritella* sp.

As Buckman pointed out (1910 : 34), the presence of a species of *Lingula* in beds of Tertiary age within the Antarctic is of interest since it extends the records of that genus to localities further south than Patagonia and the Australasian continent. With the additional material collected by the late W. N. Croft in 1947 and the single specimen figured here, from the collections of the IPS, not only is its presence confirmed, but the new record lends weight to the argument for considerably increased climatic temperatures during Lower Tertiary times in this area, as living species of *Lingula* today prefer warmer climates and are seldom, if ever, found in other than tropical seas.

The presence of a high percentage of glauconite within the Tertiary beds of Seymour Island also suggests a somewhat shallow, high energy sea area, perhaps shelf or inshore conditions.

LOCALITY. IPS loc. 16 and loc. D.515 of W. N. Croft, said to be the fossil penguin locality and equivalent to loc. 11 of Andersson (1906).

HORIZON. Lower Tertiary.

MATERIAL. The figured specimen (IPS) and ten fragments, BB.76752–9.

Superfamily **RHYNCHONELLACEA** Gray, 1848

Family **HEMITHYRIDIDAE** Rzhonsnitskaya, 1956

Genus ***HEMITHIRIS*** d'Orbigny, 1847

Hemithiris antarctica S. S. Buckman

Figs 5a–c

1910 *Hemithyris antarctica* S. S. Buckman : 13; pl. 1, figs 8, 9.

The specimen figured here is one of three almost complete examples collected from the Glauconitic Bank on Cockburn Island. It departs from the original description and figured example of Buckman (1910 : pl. 1, figs 8, 9) in its broader trigonal general outline and in having very faint radial striae. The difference in outline can be explained in terms of variability within the species which is manifest in the few specimens available here, but Buckman referred to the absence of radial striae from the surface of *H. antarctica* and used this as a point of distinction between his species and *H. psittacea* (Gmelin) and *H. woodwardi* (Adams). Close examination under a low-power microscope of the specimens available shows them to have very faint radial striae on the shell surface of both valves. The produced beak, broad sulcus and large foramen appear to be characters common to all species of *Hemithiris*.

LOCALITY. W. N. Croft's locs D.491.4 and D.526, north-eastern section of Cockburn Island.

HORIZON. Lower Tertiary. Glauconitic Bank and Pecten Conglomerate.

MATERIAL. The figured specimen, two almost complete specimens and a small fragment from the Glauconitic Bank and two well-preserved specimens and a single pedicle valve from the Pecten Conglomerate, BB.76592, BB.76749–51, BB.76601–3.

Genus ***NOTOSARIA*** Cooper, 1959

Notosaria seymourensis sp. nov.

Fig. 4

DESCRIPTION. A single crushed rhynchonellide 18 mm long, 12 mm wide, broadly oval in general outline with surface ornament of 25 coarse, rounded, radiating costae interrupted by marked concentric growth-lines becoming more lamellose towards the shell margins. A short, suberect beak is truncated by a large, subcircular foramen guarded by slightly extended deltidial plates. A striated apical plate is just visible posteriorly. [The internal characters of this specimen were impossible to define owing to the crushing of the shell.]

NAME. From Seymour Island.

LOCALITY. W. N. Croft's loc. D.492.1, south-west of Cross Valley, Seymour Island. Croft's notes (1947 : 8) record this locality as yielding traces of plant remains in hard bands and a rhynchonellide which was collected from the top of knoll in the sandy clay beds.

HOLOTYPE. The specimen BB.76590 figured here, Fig. 4.

HORIZON. Lower Tertiary.

REMARKS. In his original description of the genus *Notosaria*, Cooper (1959 : 48) distinguished it from *Tegulorhynchia* Chapman & Crespin by its different costellae and fine growth-lines. The present specimen has comparatively coarse costae and rather marked concentric growth-lines. The nature of the growth-lines, though somewhat more marked than in the type species *N. nigricans* (G. B. Sowerby), appear to conform to the pattern illustrated by Cooper (1959 : pl. 6, figs 8, 9) and show the characteristic lamellose thickening at the margins.

The presence of a specimen of *Notosaria* within the Tertiary deposits of Antarctica extends the record southwards. The only other species so far recorded from the Tertiary of the southern hemisphere are *N. nigricans* (G. B. Sowerby) and *N. sublaevis* (Thomson) from the Miocene of New Zealand.

Genus ***PLICIRHYNCHIA*** Allan, 1947

Plicirhynchia sp.

1910 *Hemithyris plicigera* Ihering; Buckman : 12; pl. 1, fig. 10.

A single damaged pedicle valve and two crushed, but complete, specimens show generic characters of *Plicirhynchia*. The single valve is subtriangular in general outline, with a produced umbo and sharp beak. The shell surface of all three specimens is posteriorly striate with anterior costae developing marginal plicae. A marked growth-line occurs at about half the length of the shell and another nearer the margins, giving a somewhat lamellose appearance to the ornament.

The specimen figured by Buckman is not instantly recognizable as *Rhynchonella plicigera* Ihering to which he assigned it, but, in view of the poor original figure of the species by Ihering (1897 : 270, fig. 7) and the fact that Buckman's specimen was equally poor, it is not easy to draw any conclusion from the comparison. Cooper (1959 : 52) had similar doubts as to their direct specific relationship. When more material is available, it may be possible to compare the two forms more effectively.

LOCALITY. W. N. Croft's loc. 491.4, Cockburn Island.

HORIZON. Lower Tertiary. Glauconitic Bank.

MATERIAL. One pedicle valve and two crushed specimens referable to this genus, BB.76746, BB.76747, BB.76748.

Genus ***TEGULORHYNCHIA*** Chapman & Crespin, 1923

Tegulorhynchia imbricata (S. S. Buckman)

Figs 11a–c

1910 *Hemithyris imbricata* S. S. Buckman : 11; pl. 1, fig. 12.

EMENDED DESCRIPTION. *Tegulorhynchia* 12·9 mm long, 17 mm wide and 6·9 mm thick. Transversely oval in general outline. Umbo short, beak sharp; foramen small, circular. Beak-ridges distinct, interarea short. Brachial valve with a low incipient median fold. Pedicle valve with a broad shallow anterior sulcus. Anterior commissure arcuate; linguiform extension long. The shell surface consists of fine, rounded, radiating costellae interrupted by numerous concentric growth-lines, giving a lamellose or imbricate appearance. [Internal characters unknown owing to lack of suitable material.]

LOCALITY. W. N. Croft's loc. D.491.4, Cockburn Island.

HORIZON. Lower Tertiary. Glauconitic Bank.

MATERIAL. The specimen BB.76593 figured here, Fig. 11a–c, and one single pedicle valve, BB.76745, from the same horizon and locality.

REMARKS. The genus *Tegulorhynchia* is the subject of a forthcoming revision of the Tertiary Rhynchonellidae by Daphne Lee of Otago University, New Zealand. In her work she includes the species *T. squamosa* (Hutton) from the Oligocene of Broken River, Castle Hill Basin, New Zealand, and *T. imbricata* (Buckman). She concludes that the two species are probably synonymous. Topotype specimens of *Tegulorhynchia squamosa* (Hutton), kindly donated by Dr Lee, have been compared with specimens collected from Cockburn Island and identified as *T. imbricata*. Although the shell ornament is similar, in all other respects the two species have little in common. The general outline of *T. squamosa* is transversely triangular to subpentagonal, whereas that of *T. imbricata* remains transversely oval. Furthermore, *T. squamosa* appears to be more robust than *T. imbricata*, with a marked posterior inflation of the brachial valve. The umbo is slightly more produced in *T. squamosa* and consequently gives rise to a more extensive interarea bounded by well-marked beak-ridges.

Buckman's citation of a rhynchonellide specimen under the name of *Hemithyris squamosa* Hutton (Buckman 1910 : 10) and the accompanying figures (pl. 1, figs 13a, b) does not justify its assignment to *Tegulorhynchia squamosa* (Hutton) as originally described (Hutton 1873 : 37). It is probable that this specimen is merely a rather poorly preserved example of *T. imbricata*, but Buckman's figure does not show the typical ornament.

Genus ***PROTEGULORHYNCHIA*** nov.

TYPE SPECIES. *Protegulorhynchia meridionalis* sp. nov.

DIAGNOSIS. Subcircular to broadly oval costellate rhynchonellide. Fold low; anterior commissure arcuate. Linguiform extension long. Umbo small, slightly produced. Beak sharp, suberect. Beak-ridges distinct. Foramen small.

NAME. Allied to *Tegulorhynchia*.

Protegulorhynchia meridionalis gen. et sp. nov.

Figs 15a–c, 16

DESCRIPTION. Small rhynchonellide, 18 mm long, 15 mm wide and 5·6 mm thick. Ornament of 32–35 fine, rounded costellae, with 8–10 on low dorsal fold and a corresponding number in shallow ventral sulcus in the anterior part of the pedicle valve. Marked concentric growth-lines become more lamellose anteriorly and thicken at the shell margins. [Internal characters unknown owing to lack of material.]

NAME. 'Southern'.

HOLOTYPE. The specimen BB.76770 figured here as Figs 15a–c.

LOCALITY. W. N. Croft's loc. D.533. On the saddle between the two peaks on Humps Islet, 63°59′ S, 57°25′ W, James Ross Island.

HORIZON. Upper Cretaceous. Lower Campanian.

MATERIAL. The holotype, BB.76770 and two other fragmentary specimens, BB.76771, BB.76772.

REMARKS. The arrangement of costellae and the lamellose nature of the concentric growth-lines are suggestive of a relationship with *Tegulorhynchia* from Tertiary and Recent localities. Similar shell ornament, however, occurs in *Rhynchonella crenifera* which was described by Stoliczka (1872–73) from the Arrialoor Groop (Campanian) of the Upper Cretaceous of Mulloor, southern India (pl. 1, figs 9 & 10 only). *Protegulorhynchia meridionalis* differs from this species in its more circular general outline and shorter or less produced umbo. Nevertheless, it is felt that the two forms are closely related and *Rhynchonella crenifera* Stoliczka is therefore here assigned, albeit tentatively, to the genus *Protogulorhynchia*, largely on similarity of general morphology and ornament.

Family **CANCELLOTHYRIDIDAE** Thomson, 1926

Subfamily **CANCELLOTHYRIDINAE** Thomson, 1926

Genus ***TEREBRATULINA*** d'Orbigny, 1847

Terebratulina buckmani sp. nov.

Fig. 9

1910 *Terebratulina lenticularis* Tate; Buckman : 28, pl. 3, fig. 4.

DESCRIPTION. *Terebratulina* 24·9 mm long, 20 mm wide and approximately 18 mm thick. Broadly oval in general outline, greatest width just anterior to mid-line. Slightly produced umbo truncated by large circular, submesothyridid, attrite foramen. Deltidial plates obscured by slightly inflated posterior part of dorsal umbo. Beak-ridges distinct; interarea moderately well defined, fairly extensive. A faint sulcus is just discernible in the anterior part of the ventral valve. The anterior commissure is incipiently uniplicate.

NAME. For S. S. Buckman.

LOCALITY. W. N. Croft's loc. D.491.5, Cockburn Island.

HOLOTYPE. The specimen BB.76594 figured here, Fig. 9.

HORIZON. Lower Tertiary. Glauconitic Bank.

REMARKS. Buckman figured a uniformly oval specimen (1910 : pl. 3, fig. 4) from the Glauconitic Bank of Cockburn Island with a maximum width about midway between the umbo and

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Fig. 4 *Notosaria seymourensis* sp. nov. **Holotype,** BB.76590, Lower Tertiary, SW of Cross Valley, Seymour Island. ×1·5.

Figs 5a–c *Hemithiris antarctica* S. S. Buckman. BB.76592, Lower Tertiary, Glauconitic Bank, northeastern section, Cockburn Island. ×1·5.

Figs 6a–c *Liothyrella lecta* (Guppy). BB.76591, Lower Tertiary, northeastern section, Cockburn Island. ×1·5.

Figs 7a–c '*Terebratella*' sp. BB.76784, Lower Campanian, Lachman Crags South, James Ross Island. ×1·5.

Fig. 8 '*Laqueus*' *cockburnensis* sp. nov. **Holotype,** BB.76595, Lower Tertiary, Glauconitic Bank, Cockburn Island. ×1·5.

Fig. 9 *Terebratulina buckmani* sp. nov. **Holotype,** BB.76594, Lower Tertiary, Glauconitic Bank, Cockburn Island. ×1·5.

Fig. 10 *Lingula antarctica* S. S. Buckman. Lower Tertiary of IPS loc. 16, Seymour Island. ×1·5.

Figs 11a–c *Tegulorhynchia imbricata* (S. S. Buckman). BB.76593, Lower Tertiary, Glauconitic Bank, Cockburn Island. ×1·5.

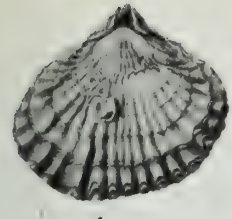
Figs 12a–c *Magella australis* (S. S. Buckman). BB.76615, Lower Tertiary, Glauconitic Bank, Cockburn Island. ×1·5.

Figs 13a–c '*Terebratula*' sp. BB.76788, Upper Cretaceous, Lower Campanian, Lachman Crags South, James Ross Island. ×1·5.

Figs 14a–c *Terebratulina* sp. BB.76789, Lower Campanian, Humps Islet, James Ross Island. ×1·5.

Figs 15a–c, 16 *Protegulorhynchia meridionalis* gen. et sp. nov. Figs 15a–c, **Holotype,** BB.76770. Fig. 16, BB.76771. Both Lower Campanian, Humps Islet. ×1·5.

a—Dorsal view. b—Lateral view. c—Anterior view.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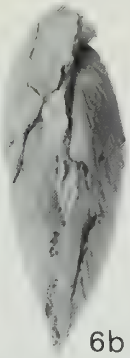
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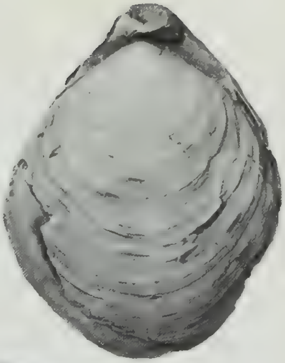
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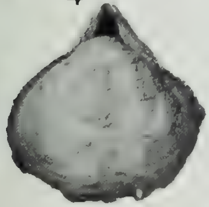
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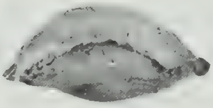
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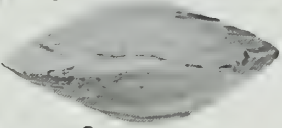
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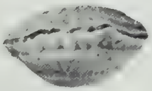
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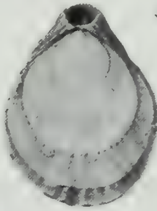
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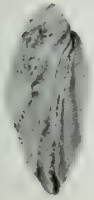
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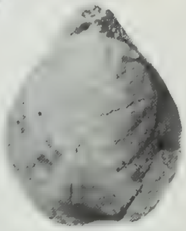
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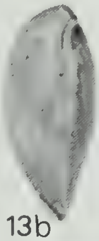
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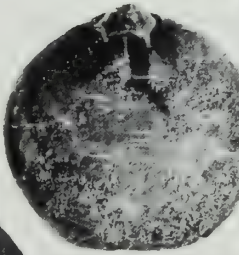
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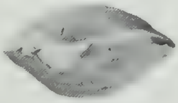
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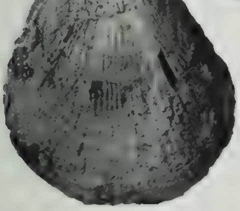
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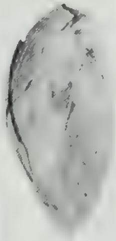
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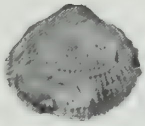
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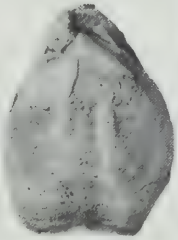
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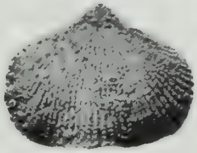
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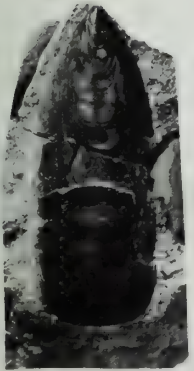
11b

14c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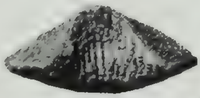
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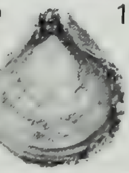
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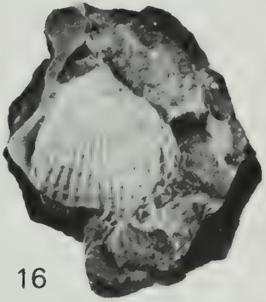
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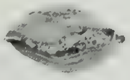
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15c

anterior commissure. In assigning the specimen to Tate's *Terebratulina lenticularis*, which was originally described from the Miocene of Aldinga, South Australia, Buckman pointed out certain discrepancies between the two forms which amounted to a difference in overall outline, beak features and sulcation of the ventral valve. He considered that the more circular outline and considerably smaller dimensions of Tate's specimens were because of their younger individual age. Comparison of the specimen figured here as *Terebratulina buckmani* sp. nov. has been made with a series of specimens in the British Museum (Natural History), which were collected and identified by R. Tate and sent to T. Davidson. The largest of nine individuals was only 8·5 mm in length. All the specimens showed less extensive interareas, and the shell ornament of fine imbricate costellae was given to more frequent bifurcation than in our Antarctic specimen.

It must be admitted that, even with careful reconstruction, the present crushed specimen could never assume the uniform outline shown in Buckman's drawing (1910 : pl. 3, fig. 4). It is possible that such differences in outline would be within the normal limits of variability of *T. buckmani* and, since neither form can be positively assigned to any other described species of *Terebratulina* within the Tertiary, it is felt that a new taxon is justifiable.

Family **TEREBRATELLIDAE** King, 1850

Subfamily **BOUCHARDIINAE** Allan, 1940

Genus ***BOUCHARDIA*** Davidson, 1850

Bouchardia antarctica S. S. Buckman

Figs 19a–c, 20a–b, 21a–c, 22a–b, 23, 24, 25, 26a–b

1910 *Bouchardia antarctica* S. S. Buckman : 16; pl. 1, figs 2, 3.
1910 *Bouchardia ovalis* S. S. Buckman : 16; pl. 1, fig. 1.
1910 *Bouchardia angusta* S. S. Buckman : 16; pl. 1, fig. 4; pl. 3, fig. 2.
1910 *Bouchardia elliptica* S. S. Buckman : 17; pl. 1, fig. 5.
1910 *Bouchardia attenuata* S. S. Buckman : 17; pl. 1, fig. 6.

EMENDED DESCRIPTION. *Bouchardia* approximately 23·8 mm long, 15·2 mm wide and 9·9 mm thick. Elongate-oval in general outline. Test thick, smooth, punctate. The umbo is short and massive with an obtuse beak dominated by a moderate to large, circular, epithyridid foramen. Extensive interarea bounded by sharp beak-ridges. The slightly concave symphytium is well exposed.

Eight to ten marked concentric growth-lines feature prominently on the almost equally convex valves. A strong carination of the pedicle valve persists anteriorly giving rise to an acute carinate anterior commissure.

Internal structures. The umbonal cavity of the pedicle valve is reduced in size by the lateral thickening of the shell and the swollen bases of the elongate hinge-teeth. A low septal ridge extends the length of the valve.

Within the brachial valve the cardinalia are thickened and fused. The area normally occupied by the hinge-trough in other Terebratellidae is filled with the thickened crural bases to form a hinge-platform. The premagadiniform brachial loop is supported by a strong, high, median septum.

LOCALITIES. W. N. Croft's locs D.498, D.504, D.506, D.507, D.515, D.519 and those of the IPS T-30, 22, 4.49; all from Seymour Island.

HORIZON. Lower Tertiary.

MATERIAL. 122 specimens, BB.76596–98, BB.76620–743, and 77 specimens in the IPS.

REMARKS. Buckman described five species of *Bouchardia* from the Younger Beds of the Tertiary deposits on Seymour Island. He distinguished them chiefly on grounds of overall general outline, some appearing more oval or elliptical and others with less acute carination of the pedicle valve.

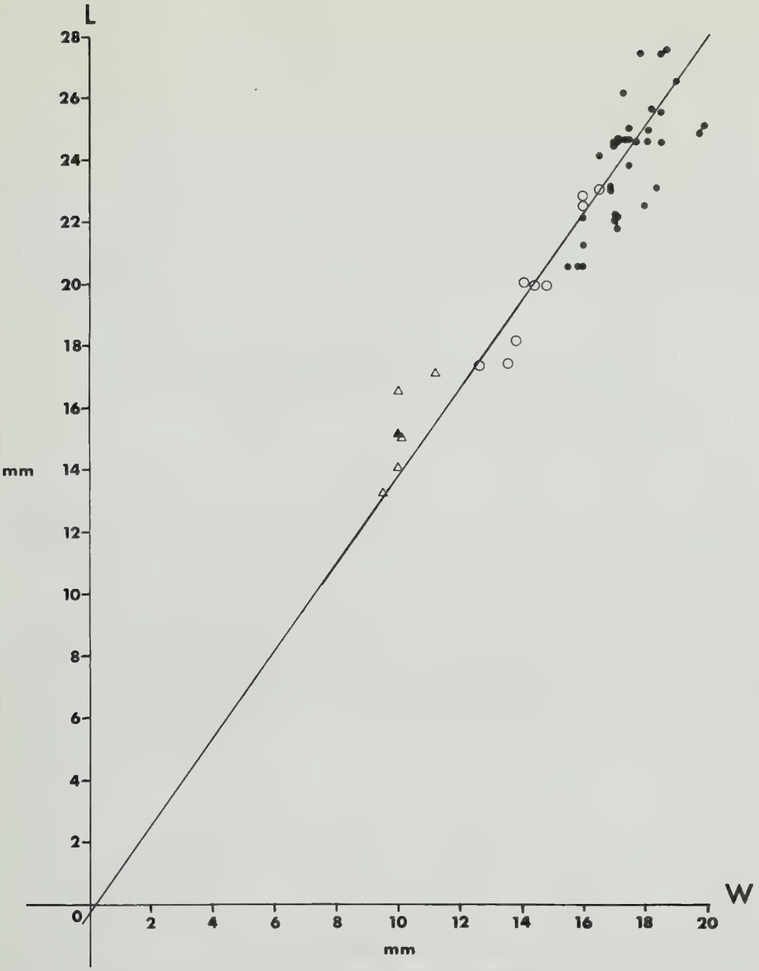


Fig. 17 Scatter diagram showing relationship of length to width in specimens of *Bouchardia antarctica* S. S. Buckman; same material as in Fig. 18. ● – IPS loc. T-30. △ – IPS locs 4, 22, 45. ○ – W. N. Croft locs.

All the specimens examined by him were collected from localities within the same geological horizons specified at that time. There is little to be said in favour of such narrow taxonomic splitting as Buckman effected, and it is more likely that, within the entire assemblage occurring in the Tertiary rocks on Seymour Island, no more than two actual species exist. Variants assigned to the species *Bouchardia ovalis*, *B. elliptica*, *B. attenuata* and *B. angusta* can be recognized in random samples from the same horizon and localities as those of the dominant species *B. antarctica*. The variation in form seems to be affected principally by the breadth of the valves or the extent of the hinge-line, those individuals with narrower or less extensive hinge-lines appearing somewhat more oval in outline.

Samples containing a mixture of specimens previously identified as *B. antarctica*, *B. ovalis*, *B. elliptica*, *B. attenuata* and *B. angusta*, together with samples of both large and small unidentified specimens collected from Seymour Island by members of the IPS expedition of 1974–75, have been measured. Taking straightforward parameters of length, width and thickness of the valves, the measurements have been plotted and are figured here as scatter diagrams, Figs 17 and 18.

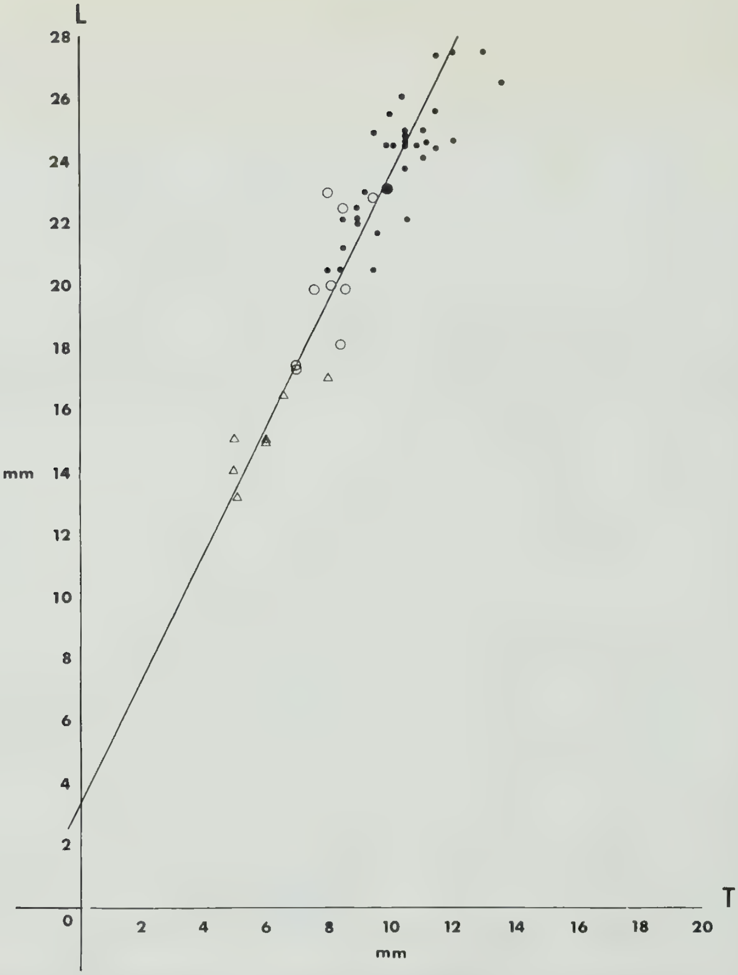


Fig. 18 Scatter diagram showing relationship of length to thickness in specimens of *Bouchardia antarctica* S. S. Buckman; same material and symbols as in Fig. 17.

The scatter diagrams clearly indicate a single species for the five taxa erected by Buckman (1910) and for the species represented by specimens collected by the IPS. These forms are here assigned to *Bouchardia antarctica* S. S. Buckman.

Ihering (1897 : 268) described *Bouchardia zitteli* from the Tertiary of Patagonia. He figured a specimen (1897 : fig. 6) which, although similar in general outline to *B. antarctica* Buckman, differs in having fewer and more pronounced concentric growth-lines and also in its faint carination of the anterior part of the dorsal valve. *B. zitteli* was again cited by Ihering (1903 : 334) and a specimen figured (1903 : pl. 3, fig. 9), together with a specimen of *Bouchardia patagonica* (1903 : pl. 3, fig. 10) which he had described from the Palaeocene of St Jorge Gulf, Pico, Salamanca, Chile. An error in the numbering of the specimens figured on the plate has caused confusion over the identification of these species. The numbers have in fact been transposed. Levy (1964 : 213) drew attention to this error when describing specimens of *B. patagonica* from the type locality.

In the same publication Levy (1964) also described and figured examples of *Bouchardia zitteli* Ihering (unfortunately misspelled as *B. zittelli*) from the Lower Tertiary of Santa Cruz, Argentina. She figured four examples (1964 : pl. 1, figs 3, 4) showing a fair range of variation in outline from broadly elongate-oval to subpentagonal in form. On the same plate (pl. 1, figs 5a–d) she figured examples of *B. transplatina* from the Miocene of the Buenos Aires area which she compared to *B. antarctica* Buckman, pointing out the difference in the carination of the ventral valve which, in *B. transplatina* Ihering, appears to be more acute than in Buckman's species. She figured a damaged specimen (figs 5a–c) with a strong carination of the pedicle valve and a corresponding sulcus in the anterior part of the brachial or dorsal valve.

Thomson (1918 : 260) had considered *B. angusta* Buckman and *B. transplatina* Ihering to be indistinguishable. As previously stated, *B. angusta* and *B. antarctica* are merely variants within the same species. It may be proved, at some future date, that *B. antarctica* Buckman and *B. transplatina* Ihering are synonyms. No examples of *B. transplatina* were available for comparative study when the present publication was being prepared and, therefore, no confirmation of Thomson's ideas was possible.

Subfamily **TEREBRATELLINAE** King, 1850

Genus ***TEREBRATELLA*** d'Orbigny, 1847

Terebratella crofti sp. nov.

Figs 27a–c

DESCRIPTION. Medium-sized biconvex pentagonal terebratellide approximately 27·7 mm long, 24·9 mm wide and 13 mm thick. Dorsal valve with moderate umbonal convexity. Median sulcus originating from about the middle of the dorsal valve and broadening anteriorly. A median septum can be seen extending from the posterior umbo to just over half the length of the dorsal valve. Concentric growth-lines appear irregularly spaced but are well defined.

The ventral valve is acutely carinate with a broad hinge-line and massive umbo truncated by a large circular, mesothyridid foramen. Beak-ridges are distinct and define an extensive, smooth interarea. Anterior commissure sulcate. Faint radiating costellae are just visible on the shell surface, becoming stronger anteriorly.

NAME. For W. N. Croft.

LOCALITY. IPS coll. loc. 4, north Seymour Island.

HOLOTYPE. The specimen figured here, Figs 27a–c. IPS, Ohio State University, U.S.A.

HORIZON. Lower Tertiary.

REMARKS. The figured specimen bears a superficial resemblance to a specimen described by Buckman (1910 : pl. 1, fig. 17a–d) as *Magasella antarctica* from the Glauconitic Bank of Cockburn Island. It differs from that species in its greater dimensions, more acutely pentagonal general outline, wider hinge-line and less acutely inflated dorsal umbo. It is somewhat similar, however, to the specimen described and figured by Ortmann (1902 : 78; pl. 14, fig. 2a, b) as *Terebratella gigantea* from the Cape Fairweather Beds, Cape Fairweather, Patagonia. Ortmann's specimen is considerably larger and has a less pentangulate outline.

Levy (1961 : 87; pl. 3, fig. 1a–c) described and figured a similar form from the Lower Tertiary of Patagonia as *Pachymagas gigantea* (Ortmann), following the assignment of that species by Thomson (1927: 286) to the genus *Pachymagas*. Levy's specimen, however, does not appear to have many of the characters associated with *Pachymagas*, such as hinge teeth with swollen bases, a produced umbo and an extensive interarea. Instead it resembles many specimens hitherto assigned to *Magellania venosa* (Solander). Nevertheless, it does bear a resemblance to the specimen described and figured here as *Terebratella crofti* sp. nov.

'Terebratella' sp.

Figs 7a–c

DESCRIPTION. Elongate-oval terebratellide 19 mm long, 14·3 mm wide and 18·1 mm thick. Shell biconvex, ornamented by 25–30 strong, rounded radiating costae, given to frequent bifurcation and interrupted by marked, step-like concentric growth-lines. The short, massive umbo of the pedicle valve is truncated by a large, circular foramen. The beak-ridges are indistinct and the interarea is poorly defined.The anterior commissure is incipiently uniplicate.

LOCALITY. W. N. Croft's loc. D.422.2, Lachman Crags South, James Ross Island.

HORIZON. Upper Cretaceous. Campanian.

MATERIAL. The single specimen BB.76784 figured here, Fig. 7a–c.

REMARKS. Although tentatively assigned to '*Terebratella*' sp., the specimen is of a distinctly *Magellania* aspect. It does not have a median fold in the brachial valve, nor does it develop a sulcus in the pedicle valve, two features which distinguish it from other costate species assigned to *Magellania.* A faint septum, extending to about half the length of the shell, is just visible in the brachial valve. Owing to the rather poor state of preservation of the specimen, there is no clear indication of the development of dental lamellae in the pedicle umbo.

The specimen was found in beds of supposedly Campanian age and from a locality recorded by Spath (1953 : 58) as both C.41370 and C.41377, from which the ammonite *Gunnarites kalika* (Stoliczka) was also recorded.

Genus *MAGELLANIA* Bayle, 1880

Magellania antarctica (S. S. Buckman)

Figs 30a–c, 31

1910 *Pachymagas antarcticus* S. S. Buckman : 21; pl. 2, figs 5–7.

EMENDED DESCRIPTION. Elongate-oval *Magellania*, approximately 54 mm long, 37 mm wide and 26 mm thick. Umbo massive, suberect, truncated by large, subcircular, mesothyridid foramen; beak-ridges attrite, fairly prominent, interarea extensive. Large conjunct deltidial plates form broad, subquadrate symphytium. Shell surface smooth with numerous fine concentric growth-lines. Anterior commissure incipiently sulcate.

Pedicle valve more acutely convex than the brachial valve and with a degree of carination posteriorly. A low median fold is developed at about midway between the pedicle umbo and the anterior commissure.

LOCALITY. W. N. Croft's locs D.491.4, Glauconitic Bank, Cockburn Island, and D.519.3, 45 m SW of headland of Penguin Bay, Seymour Island.

HORIZON. Lower Tertiary.

MATERIAL. Two damaged specimens, one almost complete, but with damaged anterior, BB.76599, and one single pedicle valve, BB.76744, showing massive, peg-like hinge teeth.

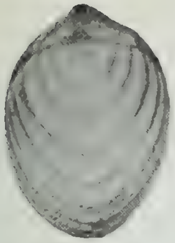
REMARKS. Although unlike other Tertiary species of *Magellania* previously described, *M. antarctica* is nevertheless comparable in size and general outline to *Magellania patagonica* (Sowerby)

Figs 19–26 *Bouchardia antarctica* S. S. Buckman. All ×1·5. Figs 19a–c, BB.76596, Lower Tertiary, Seymour Island. Figs 20a–b, 22a–b, IPS coll. 4.49, Figs 20a–b showing the atypical wide hinge-line, somewhat similar to *B. zitteli* Ihering. Figs 21a–c, IPS coll. T-30, showing slightly more parallel sides to the valves. Fig. 23, interior of brachial valve from IPS coll. T-30, showing the cardinalia and brachidium. Figs 24, stereo pair showing brachial valve with cardinalia and brachidium as internal moulds; BB.76597, Lower Tertiary of Seymour Island. Figs 25, stereo pair of a brachial valve showing cardinalia and brachidium; the hinge-line is more quadrate in outline than in the previous specimen. Lower Tertiary, Seymour Island. Figs 26a–b, a large specimen from IPS T-30, cleaned of matrix to show the massive brachial platform and strong median septum supporting the thickened brachial loop.

Figs 27a–c *Terebratella crofti* sp. nov. **Holotype**, IPS coll. loc. 4, Seymour Island. ×1·5.

Fig. 28 *Rossithyris humpensis* gen. et sp. nov. **Holotype**, BB.76773, Upper Cretaceous, Lower Campanian, Humps Islet. ×1·5.

a—Dorsal view. b—Lateral view. c—Anterior view.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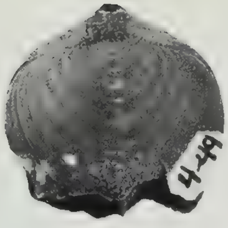
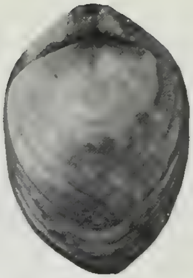


20a

22a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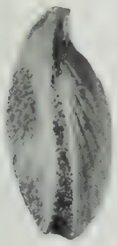
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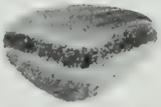
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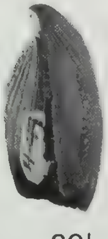
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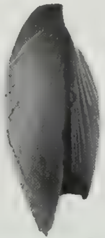
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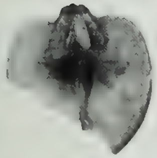
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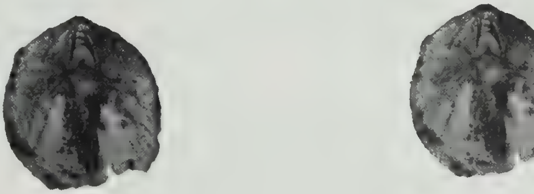
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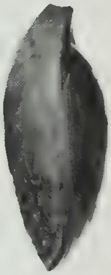
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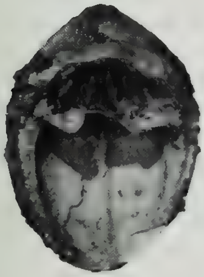
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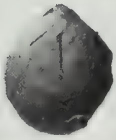
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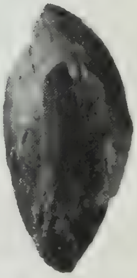
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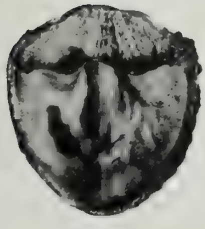
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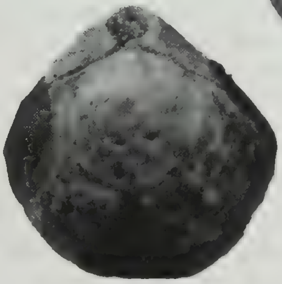
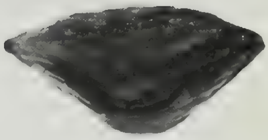

27a


27c

from the Miocene of Patagonia. It differs from this species, however, in its less acute inflation of the brachial umbo and in the incipient sulcation of the anterior commissure.

Buckman (1910) figured three specimens under the name of *Pachymagas antarcticus*. One of these figures (1910 : pl. 2, fig. 3) is said to be greatly restored. There was enough of the specimen left to remind Buckman of the species described by Ihering (1903) as *Pachymagas venter* from the Lower Patagonian of Patagonia. Buckman also pointed out that there was a similarity in form between his species and that of *Magellania venosa* as figured by Davidson (1886–88 : pl. 14, fig. 2). It is very largely on the strength of this remark and not so much on the rather poor reconstruction of Buckman's figured specimen (1910 : pl. 2, fig. 5a–c) that the specimens described and figured here as *Magellania antarctica* (Buckman) are assigned to that genus and species.

Genus ***MAGELLA*** Thomson, 1915

Magella australis (S. S. Buckman)

Figs 12a–c

1910 *Magasella australis* S. S. Buckman : 19; pl. 1, figs 14–16; pl. 3, fig. 3a–b.

EMENDED DESCRIPTION. Subquadrate to oval biconvex *Magella*, 9·7 mm long, 9 mm wide and 5·1 mm thick. Test thin, smooth, with irregularly-spaced but well-defined concentric growth-lines. Pedicle umbo massive with suberect beak dominated by large incomplete submesothyridid foramen, guarded by short discrete deltidial plates.

Brachial valve with slightly inflated umbo. A shallow sulcus develops anteriorly and gives rise to a sulcate anterior commissure.

Internal characters. Long, high median septum in the brachial valve supports a strong magelliform brachial loop.

LOCALITY. W. N. Croft's locs D. 491.4 and D.526, Cockburn Island.

HORIZON. Lower Tertiary. Glauconitic Bank and Pecten Conglomerate.

MATERIAL. Eight specimens from the Glauconitic Bank, BB.76615–22, and two from the Pecten Conglomerate BB.76623–4.

REMARKS. In his original description of the species Buckman (1910 : 19) refers to the anterior commissure as being '. . . folded to an M-Shape.' In fact, the specimen he figured (1910 : pl. 1, fig. 14c) is shown with the ventral valve uppermost which, by present-day standards, would be upside down. Thus, his description of M-shaped anterior commissure should be interpreted as W-shaped. Even so, the term does not fit the specimen figured by Buckman, nor can any specimen recently examined for the present study be described as having such a commissure.

The eight specimens examined here show a range from near rectimarginate to having a faintly sulcate anterior commissure, the sulcation developing late in the development of the shell and, therefore, being more apparent in the more mature specimens.

Thomson (1915 : 396), in his description of the genus *Magella*, suggested that *Magasella gouldi*, which Dall (1870) had described from recent seas of Japan, was based on the young stages of another terebratellide, possibly a species of *Magellania*, and, on this account, referred Buckman's species *Magasella australis* to *Magella*.

Family **LAQUEIDAE** Thomson, 1927

Subfamily **LAQUEINAE** Thomson, 1927

Genus ***ROSSITHYRIS*** nov.

TYPE SPECIES. *Rossithyris humpensis* sp. nov.

DIAGNOSIS. Small, oval, evenly biconvex laqueinid. Umbo short, foramen small, permesothyridid.

Test smooth, evenly punctate. Commissure plane. Dental lamellae short. Brachial loop laqueiniform.

NAME. From James Ross Island.

Rossithyris humpensis sp. nov.

Fig. 28

DESCRIPTION. The shell is approximately 11·6 mm long, 9·8 mm wide and 5 mm thick. Although evenly biconvex, there is a slight inflation of the umbonal region of each valve. A well-marked median septum extends just over half the length of the brachial valve. Numerous very faint concentric growth-lines appear at irregular intervals on the shell surface.

Internal characters. Pedicle valve with short subparallel dental lamellae supporting thick, inwardly-directed, peg-like hinge-teeth.

Brachial valve with a comparatively narrow, V-shaped, steep-sided hinge-trough with well-developed inner and outer socket ridges broadening anteriorly and supported by a strong, high median septum. Elongate triangular hinge-plates give rise to the descending branches of the brachial loop which quickly develop inwardly-curving crural processes.

The broad transverse band of the ascending branches, which forms the simple laqueiniform hood, appears, in transverse serial sections, at an earlier stage in *Rossithyris* than in either the Recent *Laqueus* or *Waconella* from the Cretaceous, and develops anteriorly. The descending branches connect with the median septum by means of long, thin, lateral connecting bands, Fig. 29. Similar bands are seen in transverse serial sections of *Laqueus californicus* (Koch) and *Waconella wacoensis* (Roemer) (Owen 1970 : 76–77).

NAME. From Humps Islet.

LOCALITY. W. N. Croft's loc. D.533.2 and recorded by Spath (1953 : 60) as 'on the saddle between the two peaks on Humps Islet, lat. 63°59′S; long. 57°25′W.'

HOLOTYPE. The specimen BB.76773 figured here as Fig. 28.

HORIZON. Upper Cretaceous, probably Lower Campanian. The fauna is associated with *Gunnarites antarcticus* (Weller) and *Tetragonites* sp., both ammonites previously described from localities of Campanian age within the Antarctic (Spath 1953 : 29, Howarth 1958 : 10).

MATERIAL. The holotype, BB.76773 and four fragmentary specimens, BB.76774–7.

REMARKS. Although only five specimens of this species have been collected so far, they represent a form hitherto undescribed and closely related to the Recent genus *Laqueus*. *Rossithyris humpensis* differs from that genus in that it is considerably smaller and in minor differences of brachial loop development, having a less complex but fundamentally similar expansion of the transverse band of the ascending branches. In *Laqueus* this band develops a more expansive hood with lateral lacunae. The attachment of the descending branches to the median septum occurs at an earlier stage than in any previously-described member of the Laqueinae and, in this respect, *Rossithyris* is similar to a species described below as '*Laqueus*' *cockburnensis*.

Genus ***LAQUEUS*** Dall, 1870

'Laqueus' cockburnensis sp. nov.

Fig. 8

DESCRIPTION. Brachial valve 22·4 mm long, 23·1 mm wide. Subpentagonal to elongate-oval in outline. Test thin, smooth with numerous faint concentric growth lines on external surface. A faint median sulcus is developed late in the anterior portion of the brachial valve. No cardinal process seen. Subquadrate hinge-trough, with well-developed inner and outer socket ridges, is supported by a strong, high median septum which extends to about one-third the length of the valve. The descending branches of the brachial loop are given off from the anterior part of the hinge-trough and quickly develop long, inwardly curving crural processes. A thin straight band

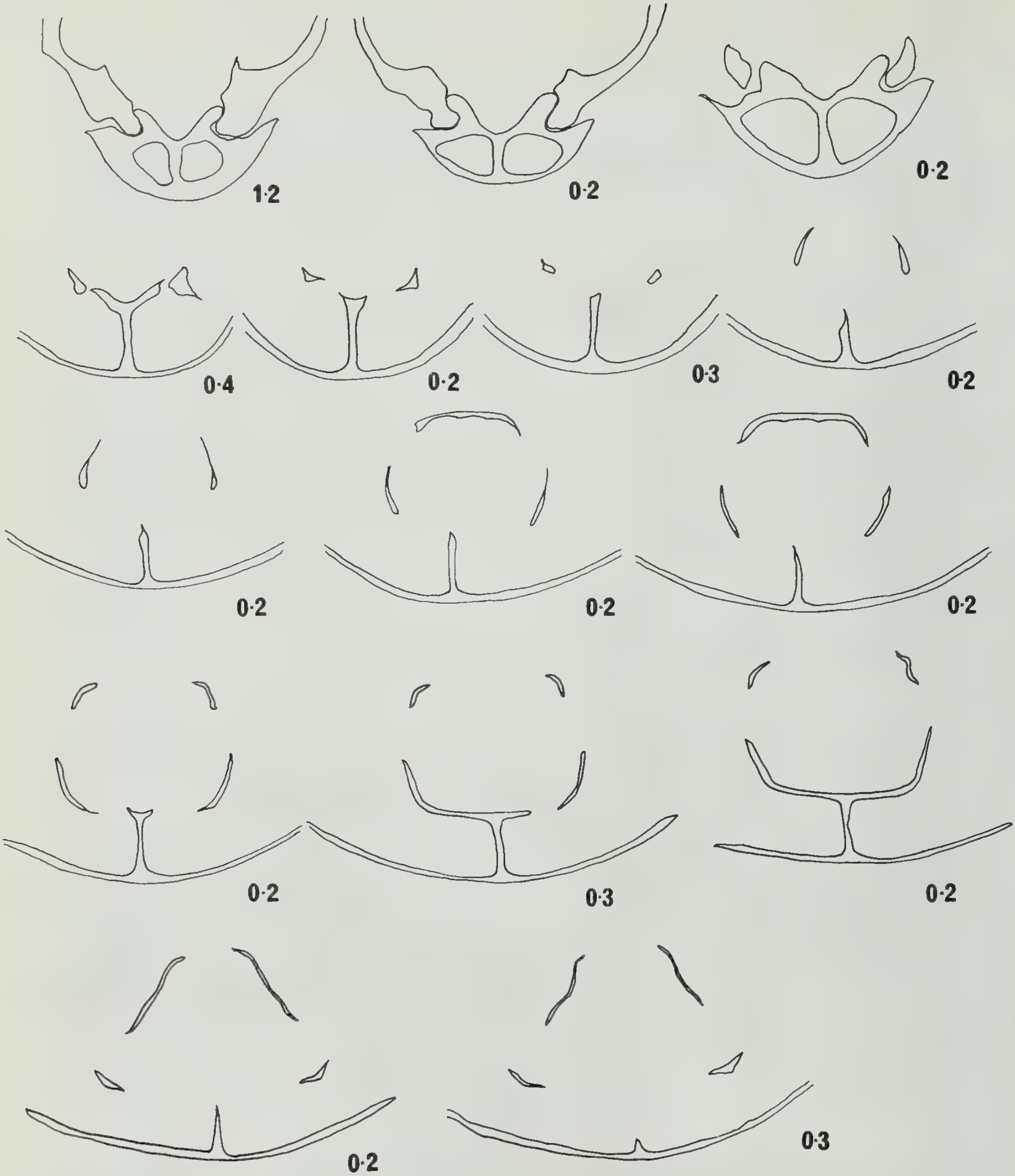

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Fig. 29 Fifteen transverse serial sections through the umbo of a specimen of *Rossithyris humpensis* gen. et sp. nov., Lower Campanian, Humps Islet. ×4.

of attachment between the descending branches of the brachial loop and the median septum develops at an earlier stage than is found in the Recent species *Laqueus californicus* (Koch). It is noted, however, that in specimens of *Laqueus vancouveriensis* (Davidson) from the waters of Naha Bay, south-eastern Alaska, an earlier attachment of loop to septum occurs and that this stage is accompanied by a less expansive or simpler development of the transverse band or laqueiniform hood in the ascending branches.

NAME. From Cockburn Island.

LOCALITY. W. N. Croft loc. D.491, Cockburn Island.

HOLOTYPE. The specimen BB.76595 figured here, Fig. 8.

HORIZON. Lower Tertiary. Glauconitic Bank.

MATERIAL. Two brachial valves and three fragmentary pedicles valves, BB.76595, BB.76785, BB.76786, BB.76787.

REMARKS. As no complete brachial loop has been preserved with any of the specimens available, it is not possible to assign the species described here to any genus beyond a broad *sensu lato* determination. It is hoped that more material will become available for further study at some future date.

The fact that there are certain morphological features which all members of the Laqueinae have in common does not imply that there is any direct relationship between '*Laqueus*' *cockburnensis* and *Rossithyris humpensis* gen. et sp. nov., described here (p. 139) from the Upper Cretaceous, Campanian of Humps Islet, Ross Island. It is interesting to note, however, that in both species the attachment of descending branches of the loop to the median septum occurs earlier than in other members of the Laqueinae.

Superfamily **TEREBRATULACEA** Gray, 1840

Family **TEREBRATULIDAE** Gray, 1840

Genus ***LIOTHYRELLA*** Thomson, 1916

Liothyrella lecta (Guppy)

Fig. 6a–c

1866 *Terebratula lecta* Guppy : 296; pl. 19, fig. 3.
1910 *Terebratula lecta* Guppy; S. S. Buckman : pl. 2, figs 1, 2; pl. 3, fig. 1.
1910 *Terebratula vitreoides* Tate; S. S. Buckman : pl. 2, fig. 3.

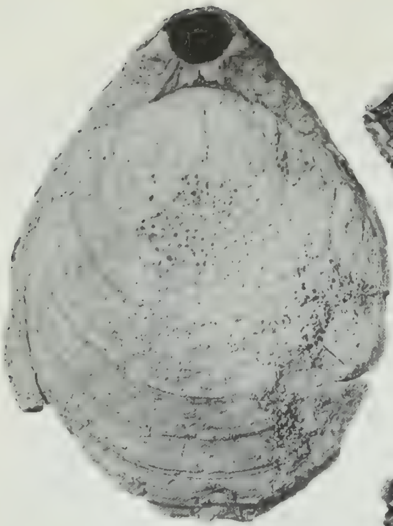
Examples of this species have been adequately described and figured by Buckman (1910) and no emendation of the original description is required.

The specimen figured here, Fig. 6a–c, is an elongate-oval terebratulide 33 mm, long, 26·3 mm wide and 12 mm in thickness. The maximum width occurs at a little over half the length of the shell anteriorly. The fine concentric growth-lines on the smooth surface of the shell are crossed by numerous faint radiating grooves. This character was included by Guppy (1866) in his original description of the species and was noted by Buckman when recording and describing the species from the Antarctic. It is thus distinct from *Terebratula vitrioides* Tenison-Woods, 1878, from the Miocene of Tasmania, which it closely resembles, and differs also from that species in its less robust appearance and less inflated brachial valve. The anterior margin of *L. lecta* is incipiently uniplicate, whereas that of *Terebratula vitreoides* is seen to develop a very faint biplication in some young and adult forms.

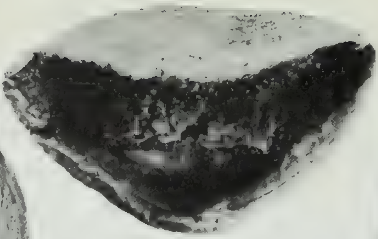
LOCALITIES. W. N. Croft's locs D.491.4, D.491.5, D.491.6 and D.525.3, Cockburn Island.

HORIZON. Lower Tertiary. Glauconitic Bank.

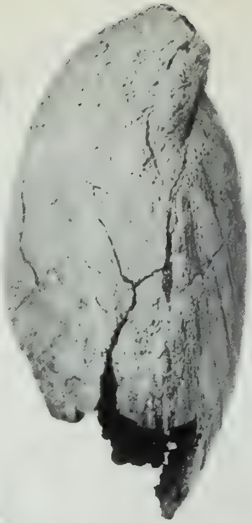
MATERIAL. Eighteen specimens and shell fragments, BB.76591, BB.76604–14, BB.76778–83.



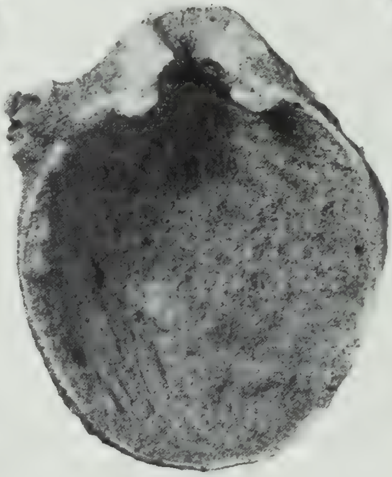
30a



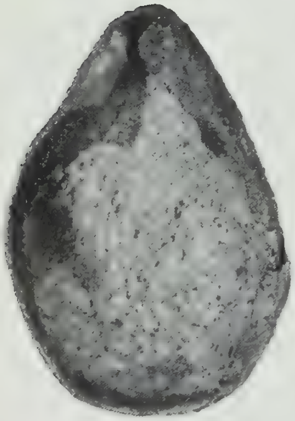
30c



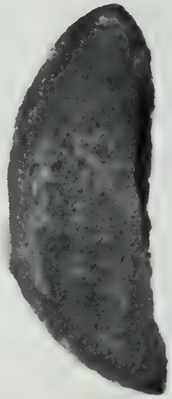
30b



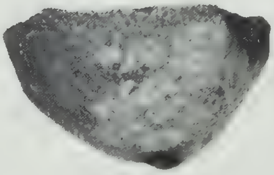
31



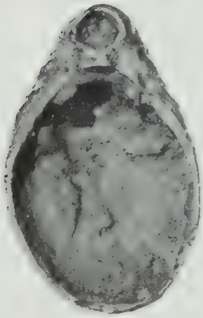
32a



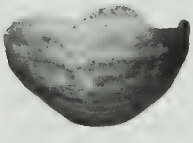
32b



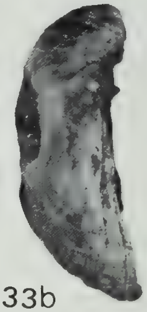
32c



33a



33c



33b

Figs 30a–c, 31 *Magellania antarctica* (S. S. Buckman). All ×1·5. Figs 30a–c, BB.76599, Lower Tertiary, Glauconitic Bank, Cockburn Island. Fig. 31, single pedicle valve BB.76744, Lower Tertiary of Seymour Island.

Figs 32a–c, 33a–c *Liothyrella anderssoni* sp. nov. Lower Tertiary, IPS coll. loc. 45, Seymour Island. ×1. Figs 32a–c, **Holotype.**

a—Dorsal view. b—Lateral view. c—Anterior view.

Liothyrella anderssoni sp. nov.

Figs 32a–c, 33a–c

DESCRIPTION. Elongate-oval *Liothyrella*, averaging 48·2 mm long, 33·1 mm wide and *c.* 24 mm thick. Test smooth with numerous irregularly-spaced, well-defined concentric growth-lines. Massive, slightly produced, pedicle umbo dominated by a large subcircular mesothyridid labiate foramen. Delthyrium subquadrate, deltidial plates conjunct. Short, slender hinge-teeth, well developed. Anterior commissure rectimarginate.

NAME. For J. G. Andersson.

LOCALITY. IPS coll. loc. 45, *c.* 2 km NE of Cross Valley, Seymour Island.

HOLOTYPE. The specimen figured here, Figs 32a–c. IPS, Ohio State University, U.S.A.

HORIZON. Lower Tertiary.

MATERIAL. Three fragmentary pedicle valves.

REMARKS. This is the first record of a species of *Liothyrella* from the Tertiary of Seymour Island. The species occurs in the top beds of the La Meseta Formation (unit IV of Elliot *et al.* 1975) and cannot be directly related to any known species of *Liothyrella* previously described. It is a robust biconvex form with a massive umbo and labiate foramen, which somewhat resembles *L. oamarutica* (Boehm, 1904) from the Miocene of Kakanui, North Olap, New Zealand, in its general morphology. It differs from that species, however, in its more elongate-oval outline or narrower development of the anterior part of the shell. The marked pedicle collar seen in *L. oamarutica* is absent in *L. anderssoni*, but the arrangement of the concentric growth-lines on the shell surface and the degree of convexity of the pedicle valve is reminiscent of that species.

In addition to the above systematic descriptions, a biplicate terebratulide of Campanian age is figured here, Fig. 13a–c. The locality is given as Lachman Crags South, James Ross Island, given in Croft's notes as D.422.2. Approximately 50 specimens said to be from the same locality can be definitely assigned to the genus *Bouchardia*. The occurrence of these specimens in beds of presumably Upper Cretaceous age leaves an element of doubt regarding the accuracy of the locality citation.

Without knowledge of the internal structures of this form, it is impossible to give any more than an arbitrary suggestion as to its generic status. It has external morphological features similar to those of a *Concinnithyris* sp. from the Middle to Upper Cretaceous of the northern hemisphere.

Conclusions

Buckman (1910 : 34) drew up a table dividing the Tertiary faunas of both Seymour Island and Cockburn Island into three main groups, as follows.

a. The Pleistocene, represented by the Pecten Conglomerate of Cockburn Island and containing a distinct fauna of *Hemithiris antarctica*, *Magasella australis* and *Magellania fontainei*.

b. Pliocene–Miocene of Seymour Island in which his *Bouchardia antarctica* and the varieties *B. ovalis*, *B. angusta*, *B. elliptica* and *B. attenuata* were dominant and *Lingula antarctica* was comparatively rare.

c. Miocene–Oligocene, represented by the Glauconitic Bank of Cockburn Island, containing *Hemithiris australis*, *H. imbricata*, *H. plicigera*, *H. squamosa*, *Magasella antarctica*, *Pachymagas antarcticus*, *Terebratula trinitatensis*, *T. bulbosa*, *T. lecta*, *T. vitrioides*, *Terebratulina lenticularis* and *T. oamarutica*.

As far as can be ascertained, there is no palaeontological evidence for the age determination of these deposits except by comparison with similar brachiopod faunas from Tertiary deposits in South America and Australasia. Buckman's descriptions and records of the species, however, were based upon poorly-preserved specimens, some of which had been greatly restored and reconstructed.

The fauna described here from similar localities on Seymour Island varies little in constitution from that described in Buckman's original work except for the addition of *Notosaria seymourensis* sp. nov., a first record for that rhynchonellide genus from as far south as Antarctica, *Terebratella crofti* sp. nov., *Magellania antarctica*, previously described and recorded only from the Glauconitic Bank, Cockburn Island as *Pachymagas antarcticus*, and *Liothyrella anderssoni* sp. nov., a new record for the genus from Seymour Island. By far the most important of these records is that of *Notosaria* since no species assigned to that genus has been recorded outside the Miocene or Recent seas.

There is no additional evidence, therefore, either to confirm Buckman's claims to the age of the deposits or to deny them. Zinsmeister (1977) records a new species of the gastropod genus *Struthioptera* from the Seymour Island Series and considered this, together with a reference to a member of the *Venericardia planicosta* group, sufficient evidence for a Late Eocene age for these beds, supporting Cranwell's (1959) data for the slightly earlier age of Palaeocene for the basal 80 m of the same deposits.

The recommendation by Elliot & Trautman (1979) that the term Seymour Island Series should be replaced by Seymour Island Group containing two major formations, La Meseta Formation and the Cross Valley Formation is accepted here, but in their description of the beds to the north of the island, little mention is made of the existence of brachiopod faunas contained within the 450 m type secion. A broad reference to invertebrate fossils and an occasional *Lingula* appear in the text but the positions within the column of examples of *Bouchardia antarctica*, which was collected extensively, are not indicated. If, at some future date, account is taken of the relative positions of the varieties of *Bouchardia* within the column, together with data on their size differences, perhaps some useful information regarding the stratigraphical significance of the brachiopod faunas can be expected.

Acknowledgements

I would like to record my sincere thanks to Dr Michael Thomson, of the British Antarctic Survey, Cambridge, and Dr D. H. Elliot, of the IPS, for their helpful co-operation; and also to Dr C. H. C. Brunton, Dept of Palaeontology, British Museum (Natural History), for reading the typescript and offering sound advice. I would also like to thank Mr Adrian Rissoné of the same department for his work with the statistical analysis.

References

Adie, R. J. 1958. Geological investigations in the Falkland Islands Dependencies since 1940. *Polar Rec.*, Cambridge, **9** (58) : 3–17.

Andersson, J. G. 1906. On the Geology of Grahamland. *Bull. geol. Instn Univ. Upsala* **7** : 19–71, 6 pls.

Boehm, G. 1904. Über tertiäre Brachiopoden von Oamaru, Südinsel Neu-Seeland. *Z. dt. geol. Ges.*, Berlin, **56** (4) : 146–150, 1 pl.

Buckman, S. S. 1910. Antarctic Fossil Brachiopoda. *Wiss. Ergebn. schwed. Südpolarexped.*, Stockholm, **3** (7) : 1–40, 3 pls.

Comacho, H. H. 1974. Biostratigrafia de las formaciones marinas del Eoceno y Oligoceno de La Patagonia. *An. Acad. nac. Cienc. exact. fis. nat. B. Aires* **26** : 39–57.

—— **& Fernandez, J. A.** 1955. La trangression en la costa Atlantica entre Comodoro Rivadavia y el curso inferior de Rio Chabut. *Revta Asoc. geol. argent.*, Buenos Aires, **11** (1) : 23–45.

Cooper, G. A. 1959. Genera of Tertiary and Recent rhynchonelloid brachiopods. *Smithson. misc. Collns*, Washington, **139** (5) : 1–90, 22 pls.

Cranwell, L. M. 1959. Fossil pollen from Seymour Island, Antarctica. *Nature, Lond.* **184** : 1782–1785.

Croft, W. N. (1947). *Notes on the geology of Cockburn and Seymour Islands.* 17 pp. Falkland Islands Dependencies Survey (internal report, unpublished).

Dall, W. H. 1870. A revision of the Terebratulidae and Lingulidae. *Am. J. Conch.*, Philadelphia, **6** : 88–168, 3 pls.

Davidson, T. 1886–88. A Monograph of Recent Brachiopoda. *Trans. Linn. Soc. Lond.* (2) Zool. **4** : 1–248, 30 pls.

Elliot, D. H., Rinaldi, C., Zinsmeister, E. J., Trautman, T. A., Bryant, W. A. & del Valle, R. 1975. Geological investigations on Seymour Island. *Antarctic Jl U.S.*, Washington, **10** (4) : 182–186.

—— **& Trautman, T. A.** 1979. Lower Tertiary strata on Seymour Island. *Proc. 37th biol. Colloq.* (Corvallis, Ore., 1976). (In press).

Guppy, R. J. L. 1866. Tertiary Brachiopoda from Trinidad. *Q. Jl geol. Soc. Lond.* **22** : 295–297, 1 pl.

Howarth, M. K. 1958. Upper Jurassic and Cretaceous ammonite faunas of Alexander Land and Graham Land. *Scient. Rep. Falkld Isl. Depend. Surv.*, London, **21** : 1–16, 5 pls.

Hutton, F. W. 1873. *Catalogue of the Tertiary Mollusca and Echinodermata of New Zealand in the collection of the Colonial Museum.* xvi + 48 pp. Wellington.

Ihering, H. von 1897. Molluscos dos terrenos terciarios de Patagonia. *Rev. Mus. paul.*, São Paulo, **2** : 217–382, 7 pls.

—— 1903. Les Brachiopodes Tertiares de Patagonia. *An. Mus. nac. B. Aires* (3) **2** : 321–348, 1 pl.

Levy, R. 1961. Sobre algunos Terebratellidae de Patagonia (Argentina). *Ameghiniana*, Buenos Aires, **2** (5) : 79–88, 2 pls.

—— 1964. Acerca de los Géneros *Bouchardiella* y *Bouchardia* (Braquiópodos) en el Terciario de Patagonia (Argentina). *Ameghiniana*, Buenos Aires, **3** (7) : 212–218, 2 pls.

Owen, E. F. 1970. A revision of the brachiopod subfamily Kingeninae Elliott. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **19** : 27–83, 14 pls, 17 figs.

Ortmann, A. E. 1902. Tertiary Invertebrates. *Rep. Princeton Univ. Exped. Patagonia* **4**, Palaeontology: 48–332, 27 pls.

Simpson, G. G. 1971. Review of fossil penguins from Seymour Island. *Phil. Trans. R. Soc.*, London, **B 5** (178) : 357–387.

Spath, L. F. 1953. The Upper Cretaceous cephalopod fauna of Graham Land. *Scient. Rep. Falkld Isl. Depend. Surv.*, London, **3** : 1–60, 13 pls.

Stoliczka, F. 1872–73. The Cretaceous fauna of southern India. IV. The Brachiopoda. *Mem. geol. Surv. India Palaeont. indica*, Calcutta, **4** (7) : 1–32, 7 pls.

Tenison-Woods, J. E. 1878. On the Tertiary deposits of Australia. *J. Proc. R. Soc. N.S.W.*, Sydney, **11** : 65–82, 1 pl.

Thomson, J. A. 1915. Brachiopod genera: the position of shells with Magaselliform loops, and of shells with Bouchardiform beak characters. *Trans. Proc. N.Z. Inst.*, Wellington, **47** : 392–403.

—— 1916. Additions to the knowledge of the Recent & Tertiary Brachiopoda of New Zealand and Australia. *Trans. Proc. N.Z. Inst.*, Wellington, **48** : 41–47, 1 pl.

—— 1918. The genus *Bouchardia* and the age of Younger Beds of Seymour Island. *Geol. Mag.*, London, (6) **5** : 258–263.

—— 1927. *Brachiopod morphology and genera* (*Recent and Tertiary*). N.Z. Board of Sci. & Art. Manual 7 : v + 338 pp., 2 pls.

Wilkens, O. 1911. Die mollusken der antarktischen Tertiar formation. *Wiss. Ergebn. schwed. Südpolarexped.*, Stockholm, **3** : 1–62.

Zinsmeister, W. J. 1977. Note on a new occurrence of the Southern Hemisphere Aporrhaid gastropod *Struthioptera* Finlay & Marwick on Seymour Island. *J. Paleont.*, Menasha, **51** (2) : 399–404.

Revision of the rugose coral *Diphyphyllum concinnum* Lonsdale, 1845 and historical remarks on Murchison's Russian coral collection.

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Synopsis

The type specimens of *Diphyphyllum concinnum* Lonsdale, 1845, which is also the type species of the important Carboniferous rugose coral genus *Diphyphyllum*, had been thought lost, but one has recently been found again, and is here redescribed. Comparison with recently erected neotypes suggests that they are only doubtfully conspecific. Remarks are given on the history of Murchison's Russian coral collections, which some authors had thought lost, and a list is given of those of his corals held in the British Museum (Natural History) collections.

Introduction

The objects of this note are to redescribe an important type specimen that has been found again, to correct the belief held by some other coral workers that Murchison's Russian corals described by Lonsdale are lost, and to give some historical background to these corals.

The type specimens of *Diphyphyllum concinnum* Lonsdale, 1845, collected by Sir Roderick Murchison from the Lower Carboniferous of the Urals, Russia (Murchison *et al.* 1845), are important because of the status of *D. concinnum* as the type species of the widespread Carboniferous rugose coral genus *Diphyphyllum*. Moreover, this genus has long been of additional problematic interest because there has always been uncertainty about its relation to the equally important genus *Lithostrotion*, with which it would seem to intergrade. In this respect the genus has therefore been the type example of the 'diphymorph' trend or condition (Smith & Lang 1930). The type specimens have been apparently missing for about half a century, but one was found again by one of us (R. F. W.) in 1972. Rediscovery provides an opportunity to give a new description and figures, rendered desirable by the need for a good transverse section and detailed confirmation of the description given originally by Lonsdale. We have done so here on the recommendation of Professor Dorothy Hill (University of Queensland, Australia). Redescription is now made additionally interesting by the recent designation of a neotype of *D. concinnum* from the type locality by Ivanovskiĭ & Shurȳgina (1975). Dr J. R. Nudds (Trinity College, Dublin) is currently preparing a detailed study of the genus and its relationship to other lithostrotionids.

The above Russian authors have stated (1975 : 14) that Murchison's Russian corals are lost, an impression which is presumably shared by some at least of other coral workers. This is only partly correct. We have found several other type specimens very recently as a result of checking carefully through material in our care, stimulated by this statement by Ivanovskiĭ & Shurȳgina. Others have never been lost at all. Several well-established taxonomic names were first used by Lonsdale for corals described by him in Murchison's collections, and a list of relevant material held by the British Museum (Natural History) is now desirable. A brief history of Murchison's coral collection is also appropriate. We are currently preparing redescriptions of other corals from Murchison's Russian travels held by the Museum.

All specimen numbers used here are register numbers of the Department of Palaeontology, British Museum (Natural History). In the remainder of this paper, the three institutions concerned

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will be referred to by their initials, MPG (Museum of Practical Geology), GSL (Geological Society of London) and the BM(NH).

It is a pleasure to acknowledge help from Dr Pierre Semenoff-Tian-Chansky (Institut de Paléontologie, Paris) on the coral terminology used by Ivanovskiĭ & Shurÿgina, and also from Dr John R. Nudds (Trinity College, Dublin); Mr R. J. Cleevely, BM(NH), has helped us on the historical matters. Dr G. F. Elliott, BM(NH), Dr Semenoff-Tian-Chansky and Dr J. Fedorowski (A. Mickiewicz's University, Poznań) kindly read the manuscript and offered helpful criticisms.

Historical note on Murchison's Russian corals

Murchison's Russian corals came to the BM(NH) by at least two routes. Some were presented by him to the MPG (which was, in effect, part of the Geological Survey and is now, as the Geological Museum, part of the Institute of Geological Sciences) of which Murchison was for a long time the Director. Others appear to have been presented to the collections of the GSL or otherwise found their way into these collections. In this connection Mr R. J. Cleevely, BM(NH), tells us that he knows of no Murchison donation of Russian material to the GSL, and has drawn our attention to the fact that Lonsdale was the Society's Curator and Librarian during the period 1829–42. All non-British material from both these large and important collections was later transferred to the BM(NH), the largest part of the material coming from these Institutions in 1880 and 1911 respectively. Woodward (1904 : 314) lists Murchison and Lonsdale in his entry for the MPG, and gives this 1880 date for the transfer to the BM(NH); see also p 231. Also on p. 314 there is an entry for Murchison, but the information given applies to material other than the present Urals corals. There was also a smaller transfer from the MPG to the BM(NH) in 1878 (R. J. Cleevely, personal communication).

The history of the transfer of the Geological Society collections is not summarized anywhere, and because of their historic interest and importance, this is now given here. In 1911 the GSL decided to relinquish its collections (Watts 1911*a*; 1911*b* : lx–lxii; GSL 1911*a*). British material was to be offered to the MPG, and 'foreign and colonial' material to the Trustees of the BM(NH) (GSL 1911*b*). Both institutions duly accepted and the collections were transferred (Watts 1912*a*; 1912*b*: lxix–lxxi). Teall (1913) reported on the transfer of the British fossil material and Woodward (1913) on the foreign fossil material. As Woodward explained, it was the intention not to incorporate any of the material received by the BM(NH) until 'the whole have been thoroughly curated, registered and studied'. This task was for some reason never completed, and the type of *D. concinnum* was found together with other material from the GSL, still unregistered. At various times, foreign specimens have been transferred from the Institute of Geological Sciences to the BM(NH). They were probably unintentionally sent to the MPG in the 1911 transfer, or were perhaps even left over from the 1880 transfer. Such reasons would account in part for the apparent loss of some of Murchison's Russian corals.

List of Lonsdale's corals from Murchison's Russian travels

The species below are listed in Lonsdale's original order using his names and quoting his specimen details, and giving his page and figure references. However, the species names themselves are given according to modern procedure. Species represented in the BM(NH) collections are shown by the listing of their specimen numbers; redescriptions are in preparation. Species not represented are preceded by an asterisk (*).

Although referred to as corals by Lonsdale, the following species discussed by him are now regarded as belonging to other groups; their details are not included here. *Stromatopora concentrica*, *Monticularia sternbergii*, *Stenopora spinigera*, *S. crassa*, *Fenestella infundibuliformis*, *F. retiformis ?*, *F. veneris ?*, *F. martis ?*.

Of the 30 coral species (excluding the above list) described by Lonsdale, the BM(NH) holds types, or figured or described specimens, of 19 (28 specimens). Four out of nine Silurian species are represented and 15 out of 19 Carboniferous species. The remaining corals unrepresented are: Silurian/Devonian (one), Devonian (one), Devonian/Carboniferous (one), Permian (one). Of the ten species founded by Lonsdale, eight are represented. Three of these are type species of genera founded by Lonsdale in this same work and still recognized today. Two of these are represented.

1. **Syringopora parallela* Fischer. Lonsdale 1845 : 591–592. 'Perimishel, south of Kaluga; Vitegra, Ilinsk on the Tchussovaya: Carboniferous limestone. Odoyef near Lichvin: Upper Devonian.'
2. *Syringopora distans* (Fischer). Lonsdale 1845 : 592–593. 'Ilinsk, on the river Tchussovaya, west of the Ural Mountains. Carboniferous limestone.' Specimens: R35936–7 (described only).
3. **Catenipora labyrinthica* Goldfuss. Lonsdale 1845 : 593. 'Isle of Dago, Upper Silurian. Top of Lower Silurian, at Naissi, in Lithuania.'
4. *Chaetetes radians* Fischer. Lonsdale 1845 : 595–596; pl. A, figs 9, 9a. 'Kaluga, and Vitegra, Borovitchi near Valdai, Carboniferous limestone.' Specimen: 26356 (figs 9, ? 9a), Kaluga.
5. **Chaetetes dilatatus* Fischer. Lonsdale 1845 : 596. 'Borovitchi; Miatchkova. Carboniferous limestone.'
6. **Chaetetes petropolitanus* (Pander). Lonsdale 1845 : 596–597; pl. A, figs 10, 10a. 'Nikolsk to Petropavlosk [sic], on the river Volkof; banks of the Siass river; ravines of Pulkovka and Popovka, south of St. Petersburgh; plateau of Czarskoe-celo; sea cliffs from Narva to Reval. Lower Silurian.'
7. *Lithodendron costatum* sp. nov. Lonsdale 1845 : 598–599, text-figs a, b. 'Perimishel, south of Kaluga. Carboniferous limestone.' Specimen: R33575 (text-figs a, b).
8. *Lithodendron annulatum* sp. nov. Lonsdale 1845 : 599, pl. A, figs 5, 5a. 'River Issetz, east of Ekaterinburg; Ilinsk, on the Tchussovaya. Carboniferous limestone.' Specimens: R35827 (figs 5, ? 5a), R35828–9 (described only).
9. **Lithodendron concameratum* sp. nov. Lonsdale 1845 : 599–600. 'River Oceter, Government of Tula. Carboniferous limestone.'
10. *Lithodendron fasciculatum* J. Phillips. Lonsdale 1845 : 600. 'River Tchussovaya, west flank of Ural mountains. Carboniferous limestone.' Specimen: R33574 (described only).
11. *Cladocora ? sarmentosa* sp. nov. Lonsdale 1845 : 600–601. 'Kamensk, east of Ekaterinburg. Carboniferous limestone.' Specimens: R49819–20 (described only).
12. *Columnaria sulcata* Goldfuss. Lonsdale 1845 : 601–602; pl. A, figs 1, 1a–1c. 'Habsal, near Reval. Lower Silurian.' Specimen: R33606 (figs 1, 1a–1c).
13. *Lithostrotion emarciatum* (Fischer). Lonsdale 1845 : 603–605, text-figs a–f on p. 603. 'Borovitchi, near Valdai. Carboniferous limestone.' Specimens: R17177 (text-figs a–c), R17178 (text-fig. f), R17180 (text-fig. d); specimen for text-fig. e not known.
14. *Lithostrotion mammillare* (Fischer). Lonsdale 1845 : 606–607, text-figs a, b on p. 606. 'Priksha (Valdai), Government of Novgorod. Carboniferous limestone.' Specimen: R17176 (text-figs a, b).
15. *Lithostrotion astroides* sp. nov. Lonsdale 1845 : 607–608, text-figs a–c on pp. 607–608. 'Pinega (sixty versts west); Carboniferous limestone. Tchussovaya banks, above Ust-Koiva; Carboniferous limestone.' Specimen: R17179 (text-figs a, b, c), Pinega.
16. *Lithostrotion floriforme* Fleming. Lonsdale 1845 : 608–610, text-figs a–c on p. 609. 'Borovitchi, near Valdai. Carboniferous limestone.' Specimen: R49833 (text-figs a–c).
17. **Favosites alveolaris* Goldfuss. Lonsdale 1845 : 610. 'Isle of Dago, Petropavlosk [sic] and Volshanka River (North Ural). Upper Silurian.'
18. **Favosites polymorpha* Goldfuss. Lonsdale 1845 : 610–611. 'Katchukof, on the Upper Belaia and Uziansk Zavod, in the South Ural Chain; Silurian. East of Alatau, South Ural; Devonian ? [sic]. Banks of the lake of Petropavlofsk sixty versts north-west from the Works of Bogoslofsk, North Ural; Upper Silurian ? [sic]'.
19. *Michelinia concinna* sp. nov. Lonsdale 1845 : 611–612; pl. A, figs 3, 3a. 'East of Ust Koiva, on the Tchussovaya. Carboniferous limestone.' Specimen: R33605 (figs 3, ? 3a).
20. *Cyathophyllum turbinatum* Goldfuss. Lonsdale 1845 : 612–613. 'Petropavlofsk, N. Ural. Upper Silurian.' Specimen: R36125 (described only).
21. **Cyathophyllum* (*Tryplasma*) *aequabilis* (subgen. et sp. nov.). Lonsdale 1845 : 613–614; pl. A, figs 7, 7a. 'The river Kakva; East side of the North Ural Mountains; Silurian. Petropavlofsk, northernmost Russo-Uralian mines. Silurian or Devonian ? [sic]'.
22. *Strombodes* sp. Lonsdale 1845 : 614–615; pl. A, fig. 13. 'Ussa River, junction with the Volga near Samara. Upper Carbon[iferous] limestone.' Specimen: R49741 (fig. 13).
23. *Cystiphyllum impunctum* sp. nov. Lonsdale 1845 : 615. 'Margin of the lake of Petropavlofsk, sixty versts north-west from the works of Bogoslofsk. Silurian.' Specimens: R36144–5 (described only).

24. **Caninia* sp. Lonsdale 1845 : 616–617. 'East of Usolie, on the Volga above Samara. Carboniferous limestone.'

25. *Caninia ibicina?* [sic] (Fischer). Lonsdale 1845 : 617–619; pl. A, figs 6, 6a–6d. 'Velikovo, between Vladimir and Kovrof. Upper Carboniferous limestone.' Specimens: R49743 (fig. 6), R49744 (fig. 6a), R49745 (fig. 6c); specimens for figs 6b and 6d not known.

26. *Stylastraea inconferta* (gen. et sp. nov.). Lonsdale 1845 : 621–622; pl. A, figs 2, 2a–2c. 'Kossatchi-Datchi, south of Miask, eastern side of the Ural Chain. Carboniferous limestone.' Specimen: R17562 (figs 2, 2a–2c).

27. *Diphyphyllum concinnum* (gen. et sp. nov.). Lonsdale 1845 : 624–625; pl. A, figs 4, 4a–4c. 'Hill of Tchirief, Kamensk, on the river Issetz, eastern side of the Ural Chain. Carboniferous limestone.' Specimen: R49740 (figs 4a, 4b, ? 4c; not fig. 4). See below.

28. *Porites pyriformis* Ehrenberg. Lonsdale 1845: 625–626. 'Isle of Dago; Petropavlofsk; Gothland; Malmoe Isle, in Christiania Bay; Upper Silurian.' Specimen: R31192 (described only), Isle of Dago.

29. **Aulopora conglomerata ?* [sic] Goldfuss. Lonsdale 1845 : 626. 'Isle of Dago. Upper Silurian.'

30. **Anthophyllum ? incrustans* [sic] (Phillips). Lonsdale 1845 : 631. 'Ust-Vaga, i.e. *débouchûre* of the Vaga into the Dwina. Permian.'

Systematic description

Class **ANTHOZOA**

Order **RUGOSA**

Family **LITHOSTROTIONIDAE**

Genus ***DIPHYPHYLLUM*** Lonsdale, 1845

TYPE SPECIES. *Diphyphyllum concinnum* Lonsdale, 1845, by original designation of Lonsdale (1845 : 624); Carboniferous, Urals.

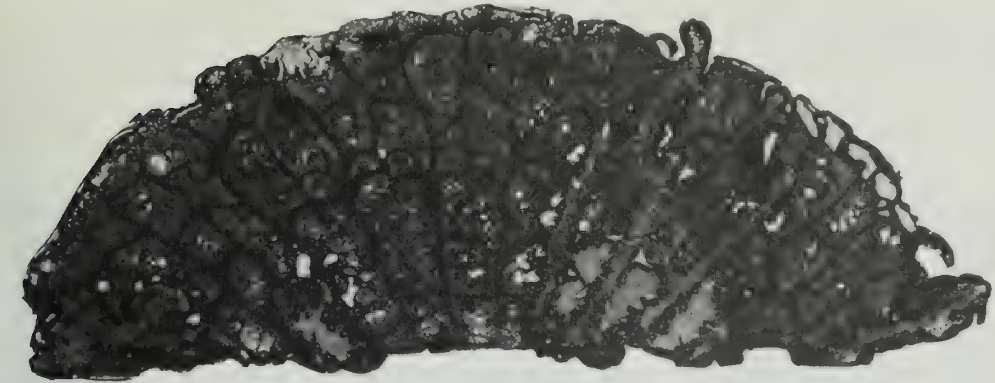
Diphyphyllum concinnum Lonsdale, 1845
(Figs 1–3)

1845 *Diphyphyllum concinnum* Lonsdale : 624; pl. A, figs 4, 4a–c.
non 1876 *Diphyphyllum concinnum* Lonsdale; Thomson & Nicholson : 123; pl. 8, figs 1, 1a [= *D. smithi* Hill].
non 1883 *Diphyphyllum concinnum* Lonsdale; Thomson : 384; pl. 8, fig. 2 [= *D. lateseptatum* McCoy].
non 1887 *Diphyphyllum concinnum* Lonsdale; Thomson : 35; pl. 4, fig. 1 [= *D. lateseptatum* McCoy].
? 1975 *Diphyphyllum concinnum* Lonsdale; [neotypes] Ivanovskiĭ & Shurȳgina : 17; pl. 2, figs 1a, b.

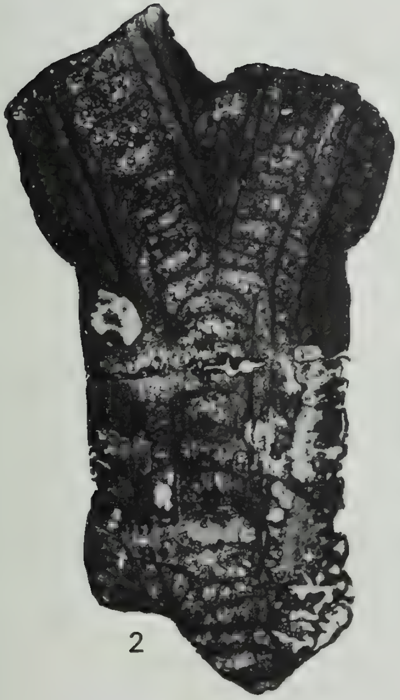
MATERIAL. One of Lonsdale's syntypes of *D. concinnum*, corresponding to his pl. A, figs 4a, 4b (possibly also 4c, but not his fig. 4). R49470.

LOCALITY. Lonsdale gives the locality as 'Hill of Tchirief [=Chiriev], Kamensk, on the river Issetz [=Iset'], eastern side of the Ural Chain'. Kamensk corresponds to the modern name, Kamensk-Ural'skiy, 56°25′ N, 61°54′ E (U.S. Army 1970). Carboniferous.

HISTORY OF THE TYPE SPECIMENS. Thomson (1887 : 33) appears to have been the last author to have worked with the type specimens of *D. concinnum*, though he did not publish explicit comparisons of his own material with the types. Blake (1902 : 28) listed the *D. concinnum* types, and this represents the most recent previous citation of Lonsdale's material. Unlike most of the other coral specimens from Murchison's Urals collection, listed in the previous section and still extant, Blake's citation shows that it definitely came from the GSL collections rather than the MPG collections. It was found in the BM(NH) in a small collection of unincorporated, unregistered GSL material representing several groups including corals, and including several other type specimens (not of Lonsdale). This collection might have arrived at a later date than the main 1911 transfer (see p. 148), or for some reason was overlooked in the original programme of incorporation which followed this transfer and was then put on one side. By the time Smith (1928) wrote his *Nemistium* paper, the specimen was thought to be lost (1928 : 114). Later authors confirmed this, including Smith & Lang (1930), who perforce recommended that the genus *Diphyphyllum* should be based on another β-form, *D. lateseptatum* (1930 : 180), which



1



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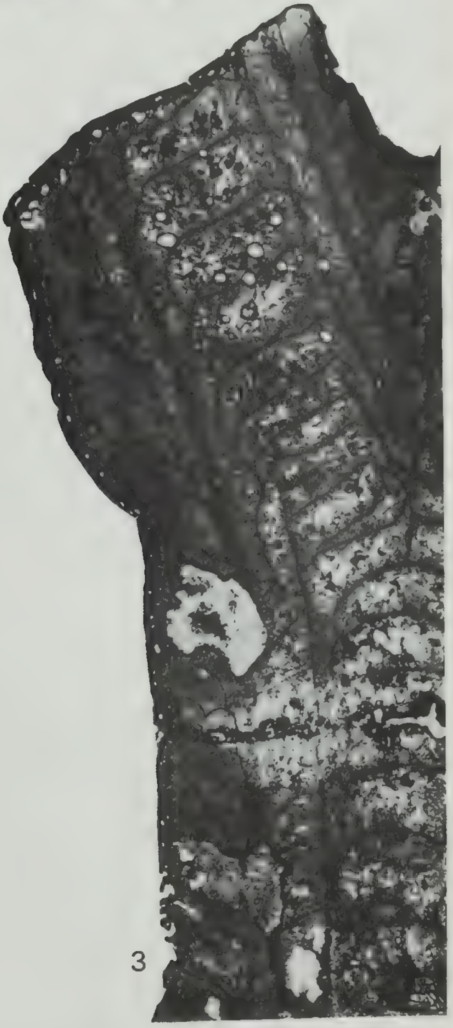

3

Figs 1–3 *Diphyphyllum concinnum* Lonsdale. Type specimen, R49470. Fig. 1, transverse section, ×16. Fig. 2, longitudinal section, ×4. Fig. 3, detail of longitudinal section, ×8.

they believed to be closely related to *D. concinnum*. (Hill revised Smith's original designation of *D. lateseptatum* as an α-form in her account of the genus (1940 : 181, 184)). The type material of *D. concinnum* had therefore been missing since 1928 at least, and possibly since 1911. Lonsdale actually based his description on several specimens, of which the one corresponding to his pl. A, fig. 4 is still missing. His fig. 4c might be the present specimen, but there is no way of knowing this.

DESCRIPTION. The specimen consists of a single corallite just under 9 mm in width, showing axial division into two corallites. Specimen length 24 mm. The apparently longitudinal section is in fact tangential, though quite close to the axis. Of the original specimen, only the section corresponding to the minor segment is to hand, and full axial details are therefore missing. Preservation is mostly good.

In the incomplete transverse section, eleven major septa are present, alternating with minors. Majors in the tabularium taper very slightly towards the axis, and they also thin marginally in the dissepimentarium to about half their tabularial thickness. Majors reach at least two-thirds of the distance to the inferred axis; minors are between one-third and a half of the length of the majors and project only very slightly beyond the dissepimentarium. Majors slightly zigzag in the tabularium and all septa slightly more so in the dissepimentarium, where there is also a slight tendency for minors to become marginally indistinct and the dissepiments to appear inosculating. The wall is lost. Dissepiments concentric to angular marginally, with innermost dissepiments more regular and smaller in the inner area of the dissepimentarium. The axial region is lost by original section cutting but a few tabular plates are visible in the most axial region.

In longitudinal section, the dissepimentarium is about two-fifths of the corallite radius. There are two marginal rows of larger, nearly horizontal dissepiments within which is an inner row of one or two very much smaller vertical dissepiments. Tabulae are in inner and outer series. Inner tabulae conspicuous, about 10 per cm in the corallite below division; mostly flat, or very slightly arched, outermost parts of each downturned steeply to rest upon the one below. Outer tabulae not conspicuous, mostly horizontal or sloping gently either inwards or outwards. No axial structures can be seen in this section. The septa are clearly seen as amplexoid spines on upper surfaces of tabulae.

Division is axial, 'parricidal'. In longitudinal section, at the point of corallite division, one axial tabula is strongly arched upward, and tabulae below it show an upward trend of increasingly arched form prior to corallite division. The new corallite wall rests directly on the summit of the most arched tabula. The full dissepimentarium structure is established within the new walls almost at the outset.

INFERRED CHARACTERS. Because of the importance of this specimen, we felt it worthwhile to attempt a reconstruction of the transverse section in order to infer some of the missing information. By extrapolating the septa axially, we found that they mostly converge at a point, which we could then use to generate a complete circular corallite circumference, making a best fit with the fragment outline by eye. This reconstructed diameter is found to be a little more than 9 mm. Using the septal pattern of the existing fragment (Fig. 1) as a template, we found the number of septa we could fit into the reconstructed outline was 52 (majors and minors). For this we assumed a fully radial septal arrangement without strongly bilateral or tetrameral features, as this is both suggested by the existing septa and approximates to the general appearance of many species of *Diphyphyllum* and *Lithostrotion*. On this reconstruction the plane of the existing tangential longitudinal section is found to be 1·25 mm off centre, i.e. it lies about two-thirds the way along the reconstructed radius from the margin. A second reconstruction of the transverse corallite section, made purely geometrically, gives a slightly larger diameter of 10 mm, over 60 major and minor septa, and a position of the plane of the tangential section rather further from the axis, at about five-eighths of the radial distance from the margin. On the basis of both reconstructions the septal number would seem therefore to be between 50 and 65 majors and minors.

The extent to which the septa extend towards the axis cannot be directly reconstructed, but those major septa which lie at right-angles to the plane of the longitudinal cut (Fig. 1) are seen to stop just short of it. The major septa would therefore have a length of at least two-thirds of the radial distance from the margin. With more material to hand this would probably prove to be variable.

Discussion. The absence of axial details is of course most unfortunate in a type specimen of *Diphyphyllum* and for this reason we have refrained from designating this specimen as the lectotype. Perhaps the remaining type material will be found in due course. Lonsdale (1845) placed great emphasis on the general absence of a columella in his own type descriptions of the present genus and species, whilst he also explained carefully how an intermittent partial columella spine was sometimes present on occasional tabulae in both his type material and numerous similar Bristol specimens. We conclude that a fully reconstructed transverse corallite section of the present specimen would belong with Smith's (1928) *Diphyphyllum* β-group. It would, however, differ from his actual figured example of the β-form (1928 : 115) in having slightly longer septa, a different dissepimentarium and a narrower inner tabularium (than the transverse figure) with rather flatter tabulae. Similar differences separate *D. concinnum* from the β-form *D. lateseptatum*, which Smith & Lang (1930, see p. 150) proposed as a type species for *Diphyphyllum* because the *D. concinnum* types were lost at the time. Differences between *D. concinnum* and *D. lateseptatum* are summarized in Table 1. We especially draw attention to the aulos-like structure, horseshoe-like dissepiments, the shorter and nearly equal minor and major septal length, and the broad inner tabulae in *D. lateseptatum*. The two species are close. however, especially with regard to septal number, transient columella and tabular form.

Table 1 Comparison between *D. lateseptatum* McCoy (in Smith & Lang 1930; Hill 1940) and *D. concinnum*

	Diphyphyllum lateseptatum McCoy	*Diphyphyllum concinnum* Lonsdale
corallite diameter	3–8 mm	9 mm (7–9·5 mm in Lonsdale)
length of major septa	*c.* $\frac{1}{4}$ corallite diameter	*c.* $\frac{1}{3}$ corallite diameter
length of minor septa	*c.* $\frac{1}{3}$ major septa ($\frac{1}{2}$ to equal in Hill)	*c.* $\frac{1}{3}$–$\frac{1}{2}$ major septa
width of dissepimentarium	narrow: *c.* $\frac{1}{8}$	wide: *c.* $\frac{2}{5}$
character of dissepiments	presence of globose, almost horseshoe-like series	horseshoe-like series not present
aulos-like structure	present	not developed
outer tabulae	concave	flat, but may slope either outwards or inwards
inner tabulae	*c.* $\frac{3}{4}$ corallite diameter	*c.* $\frac{1}{3}$ corallite diameter

In view of Dr J. R. Nudd's forthcoming revision of the whole family, we have not made an exhaustive survey of other relevant material, but the most important comparison that must be made here is that with Ivanovskiĭ & Shurȳgina's *D. concinnum* neotypes. Their vertical sections show a similar dissepimentarium but with a less frequent development of the small vertical innermost dissepiments and a narrower inner tabularium. The outer tabularium differs in being clearly trough-shaped and rather wider. Their transverse sections show a distinct but variable axial feature made up of septal lamellae, the steep sides of the inner tabulae, and even a few elements that look like tabellae. One of their corallites exhibits an axial plate. The major septa, though rarely continuous within the tabularium, frequently converge in the axial region. The authors do not give a full description, but point out that major septa 'sometimes unite in the centre forming an intermittent axial column', a feature which they relate to the development of amplexoid septa. Their figures however suggest that 'sometimes' should really be 'often'. While their figures, like Lonsdale's type, are in Smith's β-group (above), they are actually closer to Smith's (1928) *Nemistium* than they are to *D. concinnum*. Smith regarded *Nemistium* as having β-characteristics and therefore probably being a development of β-stock. The *D. concinnum* neotypes, however, are not conspecific with *N. edmondsi* Smith 1928.

In the absence of axial details in the present specimen these *Nemistium*-like features of the neotypes should be contrasted with Lonsdale's type description, which is completely unambiguous: 'The indications of an axis were very faint, being confined to the occasional appearance of a single line in the centre of the area, or to a few instances of conical irregularities in the diaphragms.' The appearance of such irregularities he relates to the axial division. While Lonsdale's observation obliges the concepts of both the species and genus to embrace an intermittent axial feature, there is as yet no evidence that his species would show quite the development of axial structures seen in Ivanovskiĭ & Shurȳgina's figures. Even if the differing degree of axial discontinuity is disregarded, the other axial features mentioned above are clearly excluded by Lonsdale's own description.

Perhaps examination of further material will show that the range of variation in Lonsdale's specimens overlaps more convincingly with that in the neotypes or that complete intergradation exists between them. We tried to test this by considering the forms placed in *D. concinnum* Lonsdale by Thomson, who strongly advocated the proper recognition of the genus. Thomson (1887) was evidently the last person to publish coral descriptions based on his having seen the type specimens before they were lost (see p. 150). We follow Hill (1940 : 184), however, in placing Thomson's 1883 and 1887 *D. concinnum* in the synonymy of *D. lateseptatum* McCoy (a different β-group form, as explained by Hill, 1940 : 181). And we believe Thomson & Nicholson's (1876) *D. concinnum* is a good α-form, and belongs with *D. smithi* Hill (1940 : 181).

Pending further studies, therefore, we would maintain that Ivanovskiĭ & Shurȳgina have provided insufficient evidence that their neotypes are the same species as Lonsdale's type, though we recognize the interest and value in presenting topotypic material. It should be noted that our conclusion is based on Lonsdale's own type descriptions rather than on any new details observed here in the type specimen.

References

Blake, J. F. 1902. *List of the types and figured specimens recognized by C. D. Sherborn, F.G.S., in the collection of the Geological Society of London.* 100+xxxii pp. London.

Geological Society of London 1911*a*. [Special General Meeting, January 25th, 1911.] *Proc. geol. Soc. Lond.* (Feb. 1911). *In*: *Q. Jl geol. Soc. Lond.* **67** : vii.

—— 1911*b*. [Special General Meeting, June 14th, 1911.] *Proc. geol. Soc. Lond.* (Aug. 1911). *In*: *Q. Jl geol. Soc. Lond.* **67** : cii–ciii.

Hill, D. 1940. A monograph of the Carboniferous rugose corals of Scotland, **3** : 115–204, pls 6–11. *Palaeontogr. Soc.* (*Monogr.*), London.

Ivanovskiĭ, A. B. & Shurȳgina, M. V. 1975. Reviziya rugoz Urala (V. Lonsdaeyl, 1845; F. N. Chernyshev, 1885, 1893; E. D. Soshkina, 1937; T. V. Nikolaeva, 1849). *Trudȳ Inst. Geol. Geofiz. sib. Otd.*, Novosibirsk, **218** : 1–44, pls 1–20. [In Russian.]

Lonsdale, W. 1845. Description of some characteristic Palaeozoic corals of Russia. Appendix A *in* Murchison, de Verneuil & von Keyserling 1845: 591–634, pl. A.

Murchison, R. I., de Verneuil, E. & von Keyserling, A. 1845. *The geology of Russia and the Ural Mountains*, **1** (Geology). xxiv+700 pp., 12 pls, 5 col. sections, 2 maps, text-figs. London.

Smith, S. 1928. The Carboniferous coral *Nemistium edmondsi* gen. et sp. n. *Ann. Mag. nat. Hist.*, London, (10) **1** : 112–120, pl. 5, text-figs.

—— & Lang, W. D. 1930. Descriptions of the type-specimens of some Carboniferous corals of the genera '*Diphyphyllum*', '*Stylastraea*', *Aulophyllum*, and *Chaetetes*. *Ann. Mag. nat. Hist.*, London, (10) **5** : 177–194, pls 7–8.

Teall, J. J. H. 1913. Fossils. *In* Strahan, A., Annual General Meeting, February 21st, 1913. Report of the Council for 1912. *Proc. geol. Soc. Lond.* (March 1913). *In*: *Q. Jl geol. Soc. Lond.* **69** : x.

Thomson, J. 1883. On the development and generic relation of the corals of the Carboniferous system of Scotland. *Proc. phil. Soc. Glasg.* **14** : 296–520, pls 1–14.

—— 1887. On the occurrence of species of the genus *Diphyphyllum*, in the Lower Carboniferous strata of Scotland, with a description of some new species and notices of varieties. *Q. Jl geol. Soc. Lond.* **43** : 33–38, pls 4–5.

—— & Nicholson, H. A. 1876. Contributions to the study of the chief generic types of the Palaeozoic corals [part]. *Ann. Mag. nat. Hist.*, London, (4) **17** : 123–128, pl. 8.

United States Army 1970. *Gazeteer No. 42 – U.S.S.R.* (2nd ed.) 7 vols. Geographic Names Division, U.S. Army Topographic Command, Washington.

Watts, W. W. 1911*a*. Annual General Meeting, February 17th, 1911. Report of the Council for 1910. *Proc. geol. Soc. Lond.* (May 1911). *In*: *Q. Jl geol. Soc. Lond.* **67** : ix–xi.

—— 1911*b*. The Anniversary Address of the President. *Proc. geol. Soc. Lond.* (May 1911). *In*: *Q. Jl geol. Soc. Lond.* **67** : lii–xciii.

—— 1912*a*. Annual General Meeting, February 16th, 1912. Report of the Council for 1911. *Proc. geol. Soc. Lond.* (Feb. 1912). *In*: *Q. Jl geol. Soc. Lond.* **68** : vii–ix.

—— 1912*b*. The Anniversary Address of the President. *Proc. geol. Soc. Lond.* (June 1912). *In*: *Q. Jl geol. Soc. Lond.* **68** : xlviii–ci.

Woodward, A. S. 1904. The Department of Geology. *In*: *The history of the Collections contained in The Natural History Departments of the British Museum*, **1** : 197–340. London, Trustees of the British Museum.

—— 1913. Fossils. *In* Strahan, A., Annual General Meeting, February 21st, 1913. Report of the Council for 1912. *Proc. geol. Soc. Lond.* (March 1913). *In*: *Q. Jl geol. Soc. Lond.* **69** : viii–ix.

Neuroptera (Insecta) in amber from the Lower Cretaceous of Lebanon

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Synopsis

Glaesoconis fadiacra sp. nov. (Coniopterygidae), *Banoberotha enigmatica* gen. et sp. nov. (Berothidae) and *Paraberotha acra* gen. et sp. nov. (Berothidae) are described from Lebanese amber.

Material and techniques

In recent years the Lebanese amber has aroused considerable interest (Schlee & Dietrich 1970, Schlüter 1976) as the oldest known amber with insect inclusions. Recently the British Museum (Natural History) received some Lebanese amber from Professor Aftim Acra of Beirut, who has been processing and studying the amber for some years.

The material has been variously dated as Aptian or Neocomian, with ages ranging from 100 to 130 m.y. (Acra *et al.* 1972, Schlüter 1976).

A preliminary examination of the insect inclusions has been made, but the plant fragments and other inclusions have not been studied. Schlee (1970) points out that the amber is difficult to handle; it is very fragile and often fragmented with many cracks developed inside the pieces. These cracks affect the clarity of the amber and its strength, and various clearing and polishing techniques have been developed to make the inclusions clearer.

The amber varies in colour from pale yellow to dark red, and in a number of examples there is evidence of some flow of the amber after the insects were trapped. In these cases parts of single insects may be separated by several millimetres or more. It is not possible to determine whether the flowing of the amber took place as the insects were trapped, resulting in the head, thorax and abdomen being separated in the same lump of amber, or whether the amber melted and flowed long after the insects were trapped. The flow within one piece of amber does not always occur in the same plane and the pieces of a single insect may be separated in three dimensions.

The amber can be examined dry or by immersion in liquids. Some organic solvents (e.g. toluene, xylene) rapidly attack the amber and usually 70% alcohol or glycerin was used. Alcohol spreads through the cracks, giving better visibility, but can lead to further fractures; it will also slightly attack the amber. Polishing the surface was done with a jewellery burnishing paste which gave satisfactory results. For greater resolution some of the more fragile pieces were embedded in plastic and then mechanically polished. In some cases minute contraction of the embedding plastic can occur as it hardens. Even slight pressure resulted in the collapse of some of the amber along the fault-cracks, distorting the block.

Other examination methods included the standard microscopical preparation techniques. The amber, after briefly soaking in xylene, was embedded in Canada balsam. This produced mixed results, generally proving satisfactory but occasionally the balsam was found partially to dissolve the amber, causing slight fragmentation of the insect specimen. A similar result was obtained by embedding in Euparal, but here the Euparal tended to clear the amber considerably, improving visibility of the specimen. The fragmentation does not destroy the fossil but results in the chitin being apparently stretched slightly in all directions by the solution effect of the mountant. This breaks the insect up into a series of small blocks which together retain the original shape of the fossil. The result is similar to a newspaper picture; at low magnification the picture is clear but at high magnification the individual particles can be seen. Some details become clearer in this manner but the specimens should always be studied fully before embedding. In this way any minor loss of detail may be more than compensated for by the improved definition of other parts.

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Specimens did not always fragment when embedded in Euparal and embedding can result in dramatically improved visibility of the specimen.

Small pieces embedded in 'Trylon' resin have been cut into serial sections on a Lastac wire saw using a 0·008-inch (0·2 mm) diamond-impregnated wire. The results have been promising but care is needed in handling the sections owing to the fragility of the amber.

Preliminary infra-red spectroscopic examination has shown a spectrum clearly distinct from that of Baltic amber and copals.

Systematics

From the amber collected by Professor Acra and at present being studied at the British Museum (Natural History), twelve orders of insects and three of Arachnida (Pseudoscorpions, Mites, Spiders) have been recognized. By far the most abundant insects in the amber are the Nematoceran Diptera, with the Hemiptera–Homoptera next, a high proportion of which are Aleyrodidae. Specimens of the following Orders have been found in the sample from Professor Acra: Thysanura, Collembola, Orthoptera, Dictyoptera, Psocoptera, Hemiptera, Thysanoptera, Neuroptera, Lepidoptera, Hymenoptera, Coleoptera and Diptera.

An account of the Lepidoptera in Lebanese amber has been published (Whalley 1977, 1978); in the present paper the Neuroptera are described.

Six specimens of neuropterous insects have been identified in the sample of Lebanese amber. These are two Coniopterygidae, three Berothidae and one fragment, probably referable to the Myrmeleonidae. No Neuroptera were recorded from Lebanese amber by Schlüter (1976), but he found specimens in resins of Cretaceous age from France (Schlüter 1975).

Family **MYRMELEONIDAE** ?

One of the specimens is only fragments of a wing (Figs 1–2), possibly a Myrmeleonid, but there is insufficient evidence to be certain of this determination. The group is known from the Triassic onwards (Crowson *et al.* 1967).

Family **CONIOPTERYGIDAE**

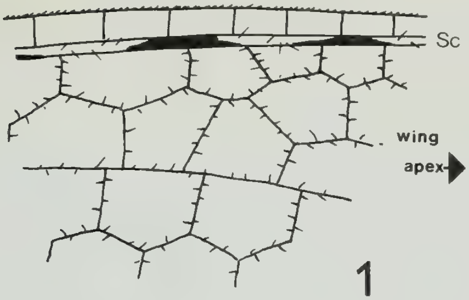
This family, including the fossils, was monographed by Meinander (1972); later he described other fossil species (Meinander 1975). One of the species he described is from Karatau (U.S.S.R.) and is generally regarded as Upper Jurassic; the other is from Siberian amber of Cretaceous age (Coniacian–Santonian). From this Siberian amber, younger than the Lebanese (Schlüter 1976), Meinander described a new genus and species of Coniopterygidae, *Glaesoconis cretica* (Aleuropteryginae), placing it in the tribe Fontenelleini. The new specimen from the Lebanese amber is congeneric with Meinander's species.

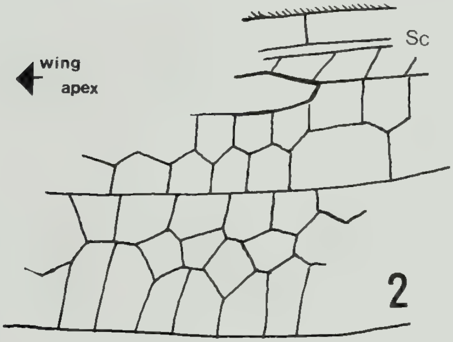
Glaesoconis fadiacra sp. nov.

Description. Front of head damaged. Flagellum with 19 segments, each slightly longer than broad. Maxillary palp five-segmented, apical segment large and broader than the others. Labial palps with enlarged terminal segment, number of labial segments unclear. Forewing about 1·7 mm (Fig. 3). Two crossveins in basal costal area. Sc_2 meeting R_1 basally of radial crossvein. Radial crossvein arises from fork of R_2+R_3. M_1 and M_2 fork, running separately to wing margin. Hindwing, partly obscured venation apparently similar to forewing. Apical r-m crossvein on branch M_1 of M_1+M_2. The abdomen is obscured but some evidence of the plicaturae on abdominal segments. [The genitalia are not visible in the specimen.]

Types. Holotype and Paratype: Lebanese amber, Lower Cretaceous. Coll. Professor Aftim Acra.

Discussion. There are three main characters which separate this species from *G. cretica*. The latter has more antennal segments (24–27). *G. fadiacra* has longer branches to R_2+R_3 and R_4+R_5,





Figs 1–2 Fragments of forewing, ? Myrmeleonid.

with their junction more basad, and the terminal segment of the maxillary palp is broader than the other segments.

With only two specimens available the validity of the intraspecific variation is uncertain. The presence of a separate M_1 on the wing margin, which is similar to *G. cretica*, is considered by Meinander to be a primitive character. In all Recent genera there are only two branches to the median vein, but three in *G. fadiacra* and *G. cretica*.

The difference between these fossil coniopterygids and Recent species is relatively small and all the main features of the family were evidently well established by the Lower Cretaceous. The presence of complex morphological features shows that the coniopterygid type of organization must have arisen well before the Lower Cretaceous, and the presence of a coniopterygid in

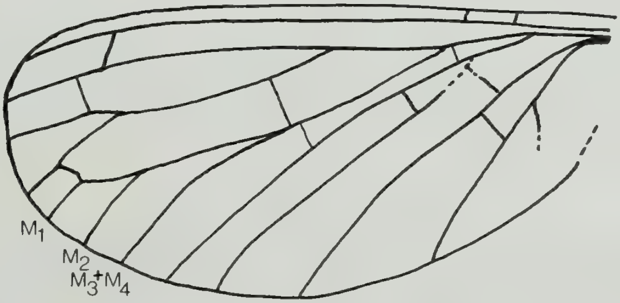


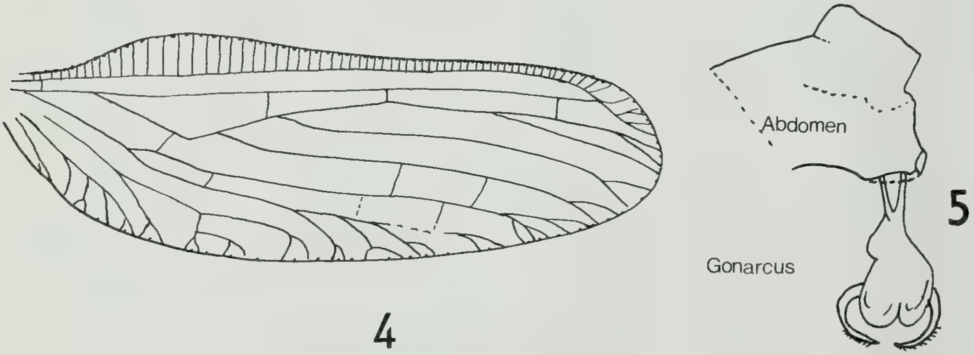
Fig. 3 Forewing, *Glaesoconis fadiacra* sp. nov. Coniopterygidae. See Fig. 7.

Upper Jurassic rocks (although with much less detail visible compared with the amber specimens) suggests an even earlier date for the separation of the Coniopterygidae from their sister group.

Family **BEROTHIDAE**

The characters given below suggest that both the adult specimens of the species described here are in the Osmyloidea (*sensu* Crowson *et al.* 1967). Riek (1970) divides the Osmyloidea, separating the Mantispoidea to include the Mantispidae, Sisyridae and Berothidae. One of the amber lacewings has characters which occur in both the Berothidae and the Sisyridae. Comparison of *Banoberotha enigmatica* sp. nov. with neuropterous fossils described from the Permian, Triassic and Jurassic does not provide any more information on its systematic position. Certainly *Permoberotha*, as illustrated by Carpenter (1954), is quite distinct.

The presence of unbranched costal veinlets in the fossil *B. enigmatica* is the most striking difference from Recent Berothidae. The hindwings are very similar, particularly with Cu_2 parallel to the hindwing margin. The anastomoses near the base of the hindwing in Recent Berothidae figured by Tjeder (1959) cannot be seen in the fossil. There are, however, sufficient characters for the fossil to be placed as a new genus and species in the Berothidae.



Figs 4–5 *Banoberotha enigmatica* gen. et sp. nov. Berothidae. Fig. 4, forewing. Fig. 5, apex of abdomen and gonarcus. See Fig. 8.

Genus ***BANOBEROTHA*** nov.

TYPE SPECIES. *Banoberotha enigmatica* sp. nov.

GENERIC DIAGNOSIS. Prothorax elongate. Forelegs cursorial. Forewing with costal veinlets unbranched. Rs and Sc fused near apex. Radial single with subparallel branches. MP bifurcate. Hindwing with Cu_2 parallel to hindwing margin.

REMARKS. The separation of this genus from Recent berothid genera is based on the costal veinlets and the differences in cross venation (Fig. 4). While the branching or otherwise of the costal veinlets is variable within one species of Recent berothids, there are usually some veinlets that are forked. In *Banoberotha* all are unbranched. The genus is placed tentatively in the Nosybinae (MacLeod & Adams 1967).

Banoberotha enigmatica sp. nov.

DESCRIPTION. Male: Wing 6 mm, wingspan about 12·5 mm. Head damaged, eyes prominent. Mouthparts not clear. Antennae with circlet of hairs on each bead-like segment. Legs broken but very hairy. Prothorax at least twice as long as broad. Forewing (Fig. 4) with many macrotrichia on veins. No recurrent humeral vein. Trichosors all round wing margin. Costal margin broader near base. Radial and subcostal veins join near apex of wing. R_1 single with four roughly subparallel branches. MA from radial (*sensu* Martynov 1928), MP forked. Cubital branched. Anal veins not clear. Hindwing frenulum group of bristles. Cubital vein almost parallel to hindwing margin. Basal area indistinct. Abdomen damaged, posterior segments as in Fig. 5. This shows the gonarcus (?) forced out; its shape is distorted by fine air bubbles around it and the figure represents the best assessment of the outline of the structure.

HOLOTYPE. Male, Lebanese amber, Lower Cretaceous. Coll. Professor Aftim Acra.

DISCUSSION. This small fossil lacewing has been compared with examples of all the Recent families and with figures of all the fossil families currently regarded as neuropterous. The fossil shows clearly the specialization reached by the Lower Cretaceous Neuroptera. The frenulum, which can be clearly seen in the fossil, has not previously been seen in fossil specimens earlier than the Tertiary, because of problems of preservation. The whole insect, except for certain venation differences, has the appearance of a Recent berothid. The abdomen is not clear enough for detailed examination but its apical shape is indicated (Fig. 5), together with what may be the gonarcus. The latter has fine spines at the apex and may well have the arms as indicated in the figure, although the shape is distorted by the air present.

Banoberotha possesses characters of both berothids and sisyrids; the simple costal veinlets are typical of Sisyridae, but all the other characters, e.g. the branched median vein of the forewing and Cu_2 in the hindwing, are typical of the Berothidae. The elongate prothorax occurs in berothids but not in sisyrids, where the pronotum is broader than long. This elongate prothorax is similar to many hemerobiids, but the fossil lacks the recurrent humeral vein and the arrangement of the radial veins differs from that family.

Amongst the Lebanese amber material collected by Professor Acra is the larger part of a neuropterous larva (Figs 9–10). While some details of the abdomen are obscured, the mouthparts quite clearly suggest a berothid larva.

DESCRIPTION. Including the long mandibles, the larva is 6–8 mm long, very hairy, probably broader in the middle and with a relatively elongate prothorax. The mandibles are long and thin, while the maxillae are shorter but broader at the base, giving a distinctly triangular look to the mouthparts. Lateral ocelli are clear; each side has five ocelli, arranged in a half-circle of four plus one ocellus ventrally placed to this group. The antennae end in a fine seta, but the number of segments is not clear. The frons is rounded with four long hairs near the anterior margin. There is a prominent epicranial suture, and the labial palps are 4- or 5-segmented. The single apical tarsal segment preserved ends without a claw, but has a trumpet-shaped empodium.

DISCUSSION. The larvae of only a few Recent species of Berothidae are known, but the most important diagnostic feature is the broad bases to the maxillae (Riek 1970), which show clearly in the fossil. No evidence for the subfamily position of this larva can be deduced since adult lacewings from two distinct Berothid subfamilies have been found in the same amber.

The final specimen from the Lebanese amber, although damaged, shows most of the characters of the Berothidae, but especially the raptorial forelegs characteristic of the endemic African subfamily, Rhachiberothinae. It is distinct from the two Recent genera but still within the subfamily Rhachiberothinae, which evidently has a long fossil history.

Genus ***PARABEROTHA*** nov.

TYPE SPECIES. *Paraberotha acra* sp. nov.

GENERIC DIAGNOSIS. Prothorax not elongate, forelegs raptorial. Forewing with Sc and R joining near apex. Trichosors on wing margin. Subcostal veinlets branched in basal third.

REMARKS. From *Rhachiberotha* Tjeder the new genus is separated by the shorter pronotum and the fusion of Sc and R near the apex. It is similar to that genus in the more medial position of the antennal sockets. In the Recent genus *Mucroberotha* Tjeder these are placed higher up, level with the upper part of the eye. The genus *Paraberotha* is placed in the Rhachiberothinae; species in this subfamily are currently known only from Zimbabwe-Rhodesia.

Paraberotha acra sp. nov.

DESCRIPTION. Wing 4 mm. Head damaged, mouth parts missing, eyes prominent. Antennae with circlets of hairs on each segment, long, with bead-like, slightly elongate, segments. Pronotum broader than long. Tip of abdomen and most of legs missing. Forelegs raptorial (Fig. 12), with two rows of teeth on femur interlocking with spines on tibia and tarsi. Teeth 21–23 in each row on femur, 10–15 long spines on tibia. Probably 5 tarsal segments, 4 visible. First segment longer than rest with long spines, segments 2–3 enlarged apically with prominent spine. Wings partially obscured. Sc and R fused near apex, separate towards base. Costal veinlets bifurcate in basal third of forewing. No recurrent humeral vein. Hindwings partially obscured but Cu elongate, parallel to hind margin.

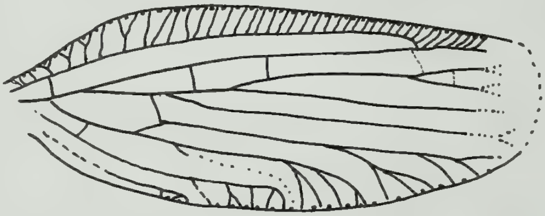


Fig. 6 Forewing, *Paraberotha acra* gen. et sp. nov. Berothidae. See Figs 11–12.

HOLOTYPE. Male (?), Lebanese amber, Lower Cretaceous. Coll. Professor Aftim Acra.

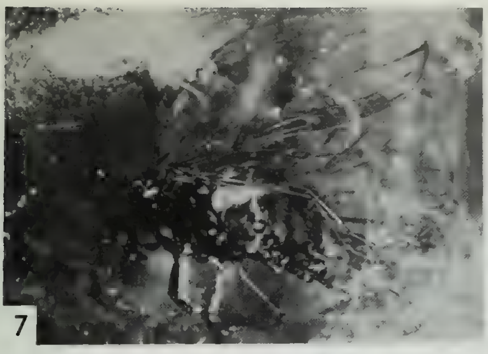
DISCUSSION. Comparison of *Paraberotha acra* with the Recent species *Rhachiberotha signifera* Tjeder shows many interesting parallels and some differences. The forewing venation is broadly similar, but the Recent species has more subcostal veinlets bifurcating and Sc and R not fusing below the apex. The teeth of the femur are very similar in Recent and fossil species, especially in their construction and insertions, and differ only in the arrangement, being alternately long and short in the fossil while rather irregular in length, though in similar rows, in the Recent species. The arrangement of teeth on the femur differs amongst the few Recent species in the Rhachiberothinae.

The overall similarity of Recent and fossil species is striking. Probably one of the most fundamental differences is in the shape of the pronotum. In most Recent species (Mantidae, Mantispidae, Rhachiberothinae), where the forelegs are modified for grasping and holding the prey, the pronotum is elongate; in the fossil *Paraberotha* it is quite clearly not elongated.

Tjeder (1959) regarded the Rhachiberothinae as a possible connecting link between the Mantispidae and Berothidae. MacLeod & Adams (1967) review this relationship in more detail and, while not agreeing with the reasons given by Tjeder, agree with his conclusions and this possible relationship.

Apart from Lebanese amber, fossil Berothids are known only from Baltic amber (Eocene/ Oligocene); these are probably in the Berothinae (MacLeod & Adams 1967). Schlüter (1978) describes *Retinoberotha stuermeri* as a new genus and species from the Cenomanian of north-west France.

Little is known of the biology of Recent Berothidae. For example, while the forelegs of Recent Rhachiberothinae are typically raptorial and are almost certainly used to catch prey, this has not actually been observed, and the modifications of the legs might even be used to assist in courtship, although I believe this unlikely.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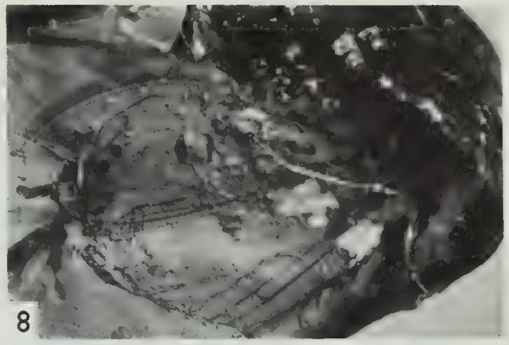
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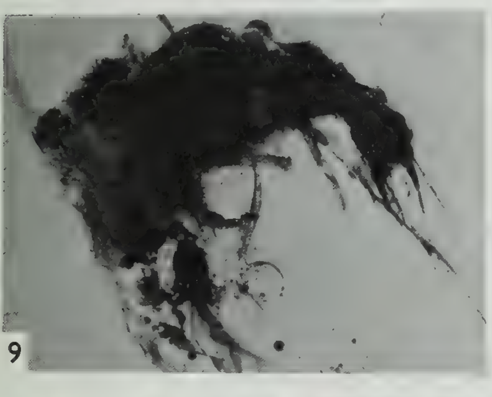
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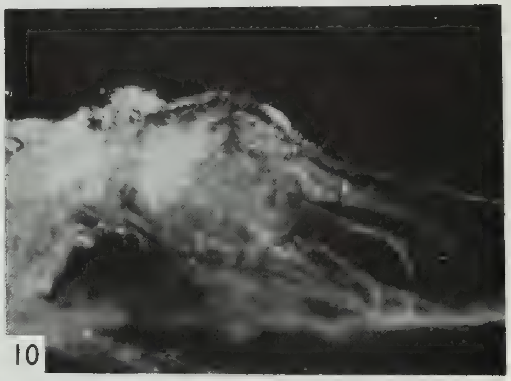
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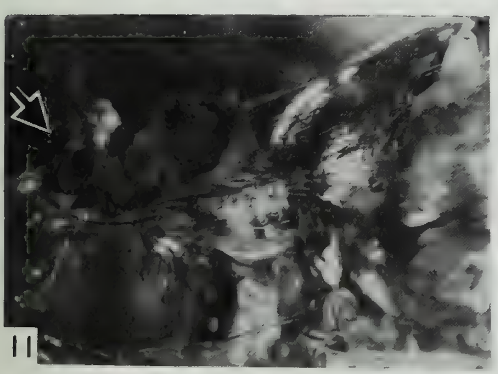
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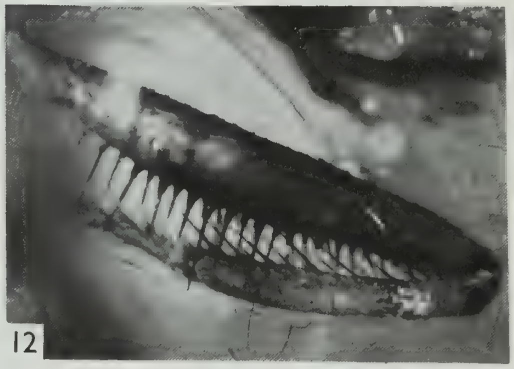
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Fig. 7 *Glaesoconis fadiacra* sp. nov. See Fig. 3.

Fig. 8 *Banoberotha enigmatica* gen. et sp. nov. See Figs 4–5.

Figs 9–10 Berothid larva. Fig. 10, enlargement of mouth parts.

Figs 11–12 *Paraberotha acra* gen. et sp. nov. Fig. 11, head and raptorial foreleg (arrowed) on left. Fig. 12, enlargement of foreleg. See Fig. 6.

When considering the faunal and floral changes since the Lower Cretaceous, the morphological stability of the Nosybinae and Rhachiberothinae is apparent. It is possible that this very stability also accounts for their apparent rarity in Recent faunas and their extremely limited distribution; while the Berothinae are widespread throughout the world, although not abundant, the Recent Rhachiberothinae and Nosybinae are rare and restricted to central and southern Africa.

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References

References marked * are not cited in the text, but are included as contributing to the bibliography of the subject.

Acra, A., Milki, R. & Acra, F. 1972. The occurrence of amber in Lebanon. *Abstr. Réun. scient. Ass. Libanaise Avmt Sci.*, Paris, **4e** : 76–77 (UNESCO).

***Carpenter, F. M.** 1940. A revision of the Nearctic Hemerobiidae, Berothidae, Sisyridae, Polystoechotidae and Dilaridae (Neuroptera). *Proc. Am. Acad. Arts Sci.*, Boston, **74** : 193–280.

—— 1954. *In* Brues, C. T., Melander, A. L. & Carpenter, F. M., Classification of Insects. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **108** : 1–917.

Crowson, R. A., Rolfe, W. D. I., Smart, J., Waterston, C. D., Willey, E. C. & Wootton, R. J. 1967. Arthropoda. *In* Harland, W. B. *et al.* (eds), The Fossil Record : 499–534. *Spec. publs geol. Soc. Lond.*, **2.**

***Krüger, L.** 1922. Berothidae. Beiträge zu einer Monographie der Neuropteren-Familie der Berothiden. *Stettin. ent. Ztg* **83** : 49–88.

*—— 1923. Neuroptera succinica baltica. *Stettin. ent. Ztg* **84** : 68–92.

***MacLeod, E. G.** 1967. Studies on the systematics of the Berothidae, 1. The genus *Sphaeroberotha* Navas with a critique of the taxonomic characters used in the Berothinae (Neuroptera). *Psyche, Camb.* **74** : 342–352.

*—— 1970. The Neuroptera of the Baltic Amber: Ascalaphidae, Nymphidae and Psychopsidae. *Psyche, Camb.* **77** : 147–180.

—— **& Adams, A.** 1967. A review of the taxonomy and morphology of the Berothidae with the description of a new subfamily from Chile. *Psyche, Camb.* **74** : 237–265.

Martynov, A. 1928. Permian fossil insects of North-East Europe. *Trudȳ geol. Muz.*, Leningrad, **4** : 1–118, 19 pls.

Meinander, M. 1972. A revision of the family Coniopterygidae (Neuroptera). *Acta zool. fenn.*, Helsinki, **136** : 1–357.

—— 1975. Fossil Coniopterygidae (Neuroptera). *Notul. ent.*, Helsinki, **55** : 53–57.

Riek, E. F. 1970. Neuroptera. *In* The insects of Australia : 472–494. Melbourne (C.S.I.R.O.).

Schlee, D. 1970. Insektenfossilien aus der unteren Kreide, 1. Verwandtschaftsforschung an fossilen und rezenten Aleyrodina (Insecta, Hemiptera). *Stuttg. Beitr. Naturk.* **213** : 1–72.

—— **& Dietrich, H. G.** 1970. Insektenführender Bernstein aus der unteren Kreide der Libanon. *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, **1970** (1): 40–50.

Schlüter, T. 1975. Nachweis verschiedner Insecta-Ordines in einem mittelkretazischen Harz Nordwestfrankreichs. *Ent. germ.*, Berlin, **1** : 151–161.

—— 1976. Die fossile Harz der gegenwärtige Erforschungsstand. *Naturw. Rdsch. Stutt.* **29** : 350–354.

—— 1978. Zur Systematik und Palökologie harzkonservierter Arthropoda einem Taphozönose aus dem Cenomanian von NW-Frankreich. *Berl. geowiss. Abh.* A **9** : 1–150.

Tjeder, B. 1969. Neuroptera planipennia, the Lacewings of Southern Africa. 2. Family Berothidae. *S. Afr. anim. Life*, Stockholm, **6** : 256–314.

Whalley, P. 1977. Lower Cretaceous Lepidoptera. *Nature, Lond.* **266** : 526.

—— 1978. New taxa of fossil and Recent Micropterigidae with a discussion of their evolution and a comment on the evolution of the Lepidoptera (Insecta). *Ann. Transv. Mus.*, Pretoria, **31** : 71–86.

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The Caradoc faunal associations of the area between Bala and Dinas Mawddwy, north Wales

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        - *Sericoidea abdita* Williams, emend. . . . 211
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Synopsis

A systematic scheme of sampling in key sections is used to provide a quantitative outline of the distribution of the total fauna in the greater part of the structurally less-disturbed, fossiliferous portion of the Lower Bala Group (and some equivalent deposits) south of Bala Lake. Sampling, data collecting and analysis techniques are discussed and derived quantitative parameters are used to describe six interrelated, brachiopod-dominated associations.

Representatives of five brachiopod, four trilobite and six molluscan genera are recorded in the group for the first time. Four new brachiopod species and a subspecies are described. These are *Paracraniops glaber* sp. nov., *Palaeostrophomena canalis* sp. nov., *Bimuria dyfiensis* sp. nov., *Protozyga musculosa* sp. nov. and *Sericoidea abdita complicata* subsp. nov.; *Parastrophinella brenchleyi* sp. nov. is also described from contemporary deposits in the NE Berwyns.

The composition of faunal associations from the Lower Bala Group is compared with the structure and characteristics of named contemporary associations in adjacent areas.

Introduction

The researches presented here are linked to a reappraisal of the geology of the Llanuwchllyn to Llanymawddwy area presented elsewhere (Lockley 1980). The present paper is principally concerned with the quantitative description of faunal assemblages and associations found in the fossiliferous upper part of the lower to middle Caradoc succession between Bala and Dinas Mawddwy. To this end a series of suitable sections were chosen for detailed examination, at more or less regular intervals along a 20 km portion of the strike belt shown in Fig. 1 (inset). Laterally spaced sample sites provide a framework in which to examine the relationships between faunal distribution patterns and vertical and lateral facies changes.

At each of the twelve localities shown in Fig. 1 a series of from 3 to 84 samples were collected at regular, measured vertical intervals. Horizons from which samples were derived are informally referred to – in conjunction with sample numbers – as 'beds'; e.g. 'bed H1' (Fig. 4) refers to the horizon from which the material of sample H1 was derived.

Where exposure permitted, including key localities such as type sections, beds were extensively sampled; at remoter, less well-exposed sites fewer samples were recovered. In all, 250 collections, totalling 1·5 metric tons of rock, were made from the twelve named sections and subjected to thorough analysis employing the methods described below. All identifiable material was assigned to its respective taxon and counted; in all some 25 000 individual specimens were examined, in addition to numerous fragmentary remains. The resultant tabulated data are presented here as the basis from which further extrapolation and inference is derived. A limited quantity of biometric data is presented in conjunction with the taxonomic descriptions; additional information is given in my unpublished thesis (Lockley 1977). Regional cleavage caused the deformation of a large proportion of the material, prevented some accurate measurement and in some cases even identification.

In the course of mapping the Llanuwchllyn to Llanymawddwy area (Lockley 1980) a few important specimens were recovered from various localities other than those shown in Fig. 1; these, together with new material from the main sections, are described in the taxonomic part of this paper. Sample numbers not prefixed with a consonant (or consonants) correspond to map locality numbers on the author's field maps (1 : 10 000) and generally refer to isolated outcrops or poorly exposed parts of minor sections; these numbers fall between 1 and 1162, and in certain cases have a suffix (e.g. A or B).

Full taxonomic descriptions are confined to the new Brachiopoda from this region and to a single new form from the Berwyns. Other figured material, including representatives of the Trilobita and Mollusca, is distinguished either by being previously unknown or undescribed in the Caradoc succession of this area or in having a particular stratigraphical significance (e.g. a considerably extended stratigraphical range). Numbers BB92200–BB92264 are used for the Brachiopoda, It.14294–It.14309 for the Trilobita, PL 4440–PL 4451 for the Bivalvia and PG 5022, C 81324, E 53698 and E 67750 for four other miscellaneous specimens; all other material is housed in the National Museum of Wales under accession number NMW 79.5G.

Conclusions are confined to correlative comparisons between the faunal assemblages and associations described here and the known contemporary faunas and named communities elsewhere. Brief comments on the definition of contemporary faunal associations (and communities) are also included where appropriate.

Stratigraphy

The stratigraphy of the Lower Bala Group was outlined by Bassett *et al.* (1966), who recognized four formations within the group in the Bala area (Fig. 1). Recognition, and indeed definition, of these formations is considerably facilitated by the occurrence of distinctive ash members within the succession. In contrast, however, the monotony of the entirely argillaceous Hengae Group described by Pugh (1923, 1928) in the Corris and Dinas Mawddwy areas is broken only by the black graptolitic shales of the Nod Glas Formation which represent the uppermost 20 m of the group.

Although Pugh (1929) attempted detailed correlations between the Bala and Dinas successions in the intervening Llanuwchllyn to Llanymawddwy area, his efforts have recently been shown to be at best imprecise and at worst quite inaccurate (Lockley 1977, 1980). Stratigraphical revisions of the succession in the Llanuwchllyn to Llanymawddwy area have not only been

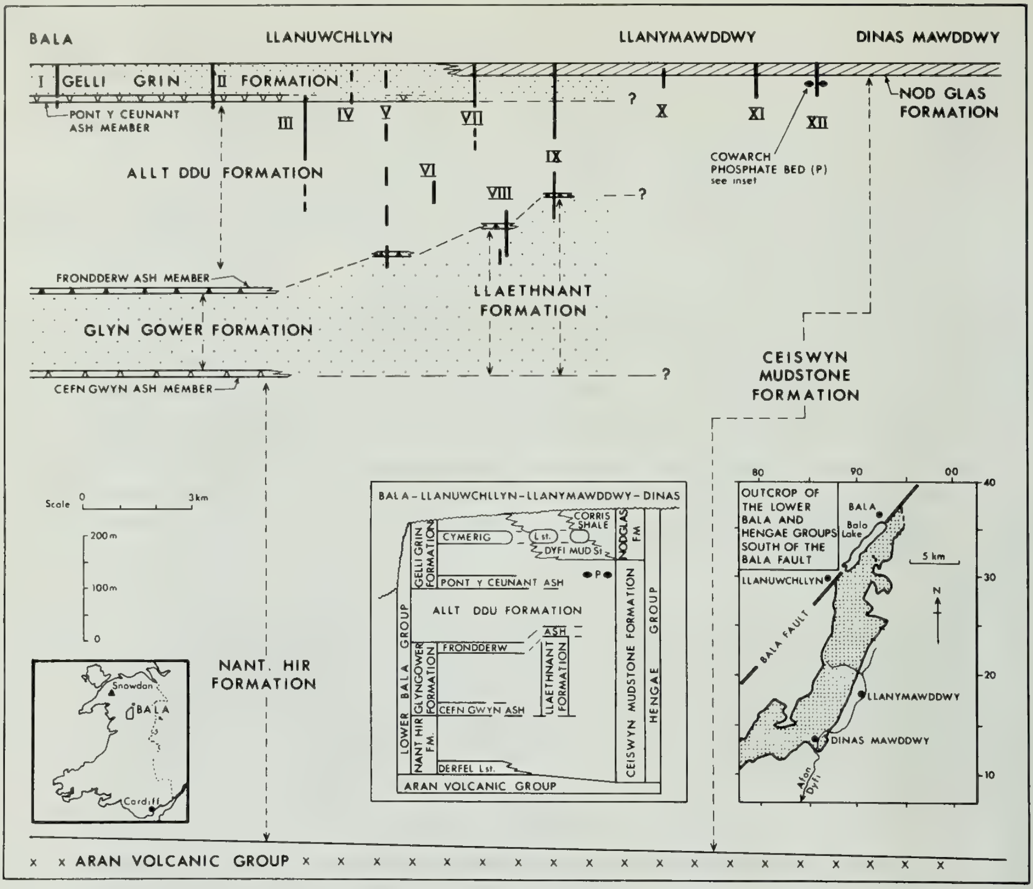

BALA
LLANUWCHLLYN
LLANYMAWDDWY
DINAS MAWDDWY
I
GELLI GRIN
II FORMATION
PONT Y CEUNANT ASH MEMBER
III
IV
V
VI
VII
VIII
IX
X
XI
XII
?
NOD GLAS FORMATION
COWARCH PHOSPHATE BED (P) see inset
ALLT DDU FORMATION
FRONDDERW ASH MEMBER
LLAETHNANT FORMATION
GLYN GOWER FORMATION
CEFN GWYN ASH MEMBER
CEISWYN MUDSTONE FORMATION
NANT HIR FORMATION
Scale 0 3km
200m
100m
0
Snowdon
BALA
Cardiff
BALA-LLANUWCHLLYN-LLANYMAWDDWY-DINAS
CORRIS SHALE
CYMERIG
L st.
DYFI MUD St
GELLI GRIN FORMATION
NODGLAS FM
PONT Y CEUNANT ASH
P
ALLT DDU FORMATION
ASH
FRONDDERW
GLYNGOWER FORMATION
LLAETHNANT FORMATION
CEFN GWYN ASH
NANT HIR FM.
DERFEL Lst.
LOWER BALA GROUP
CEISWYN MUDSTONE FORMATION
HENGAE GROUP
ARAN VOLCANIC GROUP
80
90
00
40
30
20
10
OUTCROP OF THE LOWER BALA AND HENGAE GROUPS SOUTH OF THE BALA FAULT
BALA
Bala Lake
5 km
N
LLANUWCHLLYN
BALA FAULT
LLANYMAWDDWY
DINAS MAWDDWY
Afon Dyfi
ARAN VOLCANIC GROUP

Fig. 1 Scale representation of sampled sections (solid vertical bars I–XII) in the fossiliferous upper part of the Lower Bala and Hengae Groups between Bala and Dinas Mawddwy. I, Gelli-grîn type section. II, Maes-Meillion section. III, Craig y Gath. IV, Lledwyn Bach. V, Ty nant. VI, Beudy Isaf. VII, Nant Tan y Bwlch. VIII, Afon Twrch. IX, Craig Ty nant section at Rhiw March. X, Pistyll Gwyn. XI, Y Ceunant. XII, Aber Cowarch. Insets (left, centre and right) respectively show regional setting, local stratigraphy and local geographical and geological setting.

effected by the discovery of outcrops representing distal extensions of the Frondderw Ash but have also been considerably facilitated by detailed examination of the faunal succession in sections throughout the area. The stratigraphical revisions (Lockley 1980) are summarized in Fig. 1 (inset).

The Llaethnant Formation is proposed as a name for a thick group of alternating mudstones and siltstones which, in addition to representing a different facies from the stratigraphically thinner Glyn Gower Formation, is not necessarily the chronostratigraphical equivalent of that unit.

The base of the Allt Ddu Formation, defined, following Bassett *et al.* (1966) as the base of the Frondderw Ash member, is accurately located as far south as Rhiw March in the Dyfi Valley. Similarly the base of the Gelli-grîn Formation is accurately located as far south as this locality. The greater part of the Nod Glas Formation (between Aber Cowarch and Rhiw March) is shown to be equivalent to the upper part of the Gelli-grîn Formation and to include the distal portions of the Cymerig Limestone member which becomes discontinuous towards the south.

Distinctive lateral changes in the Nod Glas facies in the area in question have resulted in the subdivision of the formation into two members which both represent facies of a diachronous nature. The Dyfi Mudstone is dominated by a distinctive *Sericoidea*-dominated fauna and the Corris Shale is characterized by being generally unfossiliferous except for local graptolitic assemblages.

Aims, sampling procedures and data analysis

The primary aim of this study has been to name and describe quantitatively the Caradoc faunal associations and assemblages found between Bala and Dinas Mawddwy, and to compare these with contemporary associations outlined by Williams (1973) and described by Pickerill & Brenchley (1979). Thorough sampling provides a census of the fossil faunas, whether representative of various biocoenoses or thanatocoenoses, which furnishes data from which recurrent combinations of taxa may be noted. Where similar combinations of taxa show chronological (stratigraphical) and geographical persistence in like facies (which lack current-produced sedimentary structures) they are referred to as 'associations' and considered to resemble disturbed neighbourhood assemblages (*sensu* Scott 1974) or *in situ* communities. Such 'associations' predominate in the area considered here. Where clearly transported shelly deposits are noted they are categorized as 'assemblages'.

Collecting techniques

Bulk samples of rock (mean weight 6 kg) were collected at vertical intervals varying from 0·5 m to > 3 m, depending on the extent of the section and the faunal content. It was found to become increasingly impracticable to collect large, closely-spaced samples as the succession got progressively less fossiliferous, as in some parts at lower horizons of the Caradoc of this area, so discretion in the choice of sample interval was exercised. However, in general it was necessary to collect a larger sample in poorly fossiliferous rocks to recover a representative number of specimens. In the six most thoroughly sampled sections (i.e. numbers I, II, III, VII, VIII and IX of Fig. 1) a mean sample interval of 2·75 m was employed for a total of over 500 m of section. Locally, as in the perfectly exposed fossiliferous upper 135 m of the Rhiw March section (IX), a smaller mean interval was employed, in this case 1·75 m.

To eliminate preferential collecting biases all samples were 'broken up' on a rock crushing machine in such a way as to ensure that all the fossils or fossil fragments were retained for identification purposes. All rock fragments were reduced to a size of 1–2 cm^3 before being discarded if unfossiliferous. With the crushing machine (a converted fly press) it was easy to reduce fossiliferous rocks to a series of chips only fractionally larger than the individual fossils themselves which, in this case, generally approximated to the above chip size. All extracted identifiable specimens were then examined under a binocular microscope and counted, totals for each taxon being considered to represent random samples of residual fossil species populations.

Faunal densities

Essentially only two types of faunal density may be calculated, density per unit volume of rock or density per unit area of bedding plane. Neither method is entirely adequate for the analysis of more than a limited variety of fossiliferous lithologies. Volumetric densities are more suited for the expression of faunal densities in homogeneous (or isotropic), poorly-bedded strata, whereas areal densities better describe the density of fossils on bedding planes in strata where the rock fabric is essentially anisotropic. Both methods are size dependent; i.e. the mean size of the fossils controls the mean number of specimens per unit area. The calculation of areal and volumetric densities produces more accurate results when applied to relatively low density assemblages and associations; it becomes more difficult to derive accurate measurements from high-density deposits such as shell beds. The practical problems of accurate counting increase with the density of specimens in the rock.

Not only are contemporary sections of varying lithology likely to require different methods of density measurement, but within the same section it may be necessary to apply alternative methods of density evaluation at successive horizons. In the present study it was primarily volumetric densities which were calculated, although a few areal density measurements were obtained from well-defined bedding planes (Fig. 2). The volumetric densities calculated for the two sections shown in Fig. 2 are a useful guide to the faunal content (i.e. density of fossils) in the sequence at successive horizons. For example, the 'faunal depletion' zone described by Bassett *et al.* (1966 : 236) is graphically illustrated and shows a marked contrast to the fossiliferous horizons of the overlying Gelli-grîn Formation, which include the dense accumulation of small *Sericoidea* valves indicated.

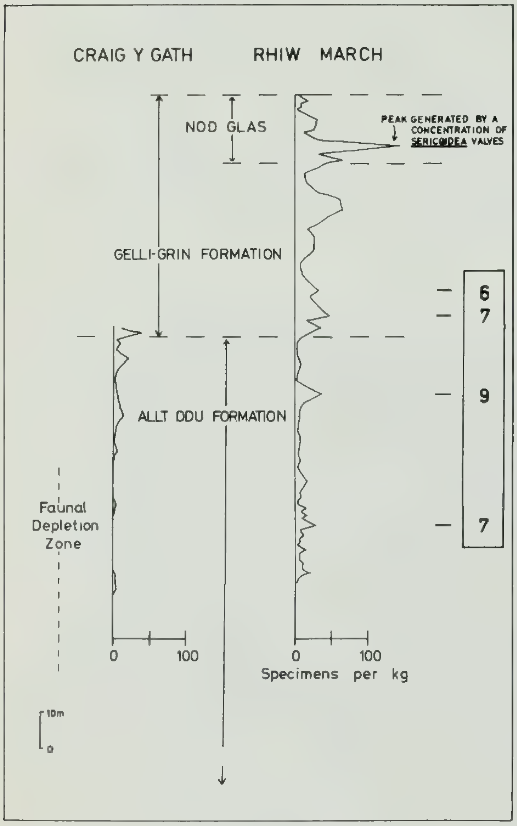


Fig. 2 Density of fossils per kg in the Craig y Gath and Rhiw March sections. Box (right) contains counts of specimens per 10 cm² on bedding planes in the latter section.

The use of volumetric density measurements in this study was preferred not only because of the disposition of fossils in the rock (i.e. generally scattered throughout rather than concentrated on easily sampled bedding planes) but also because of the strong regional cleavage inclined at a high angle to bedding, which almost invariably has the effect of breaking up bedding planes to the extent that a complete sample of more than 100 cm² is hard to obtain; the mean area of the four bedding surface samples shown in Fig. 2 is only 25 cm². The single most significant effect of cleavage on sampling procedure in the area under study is that rock splits so as to produce a sample representing a vertical range of strata extending at least 15 cm above and below any given horizon. In effect the vertical range of a sample approximates to 0·3 m.

Volumetric and areal density measurements may be compared and shown to have consistent relationships. Theoretical considerations and empirical observations support the validity of relating the two methods of evaluation. It is easily shown that 1 kg of rock (400 cm³ at a density of 2·5 g/cm^3), if broken into cubic chips between 2 cm^3 and 1 cm^3, will expose a surface area of between 600 cm^2 and 1200 cm^2 of which one third of the area (200–400 cm^2) will represent surface area in the horizontal (bedding) plane. Empirical observations by the author and Dr J. M. Hurst (personal communication 1977) have consistently shown that, when measuring the surface area of exposed bedding plane during the 'breaking up' of weighed samples, about 400 cm^2 of fresh surface is exposed for each kilogram of processed rock. When processing homogeneous, poorly-bedded lithologies it is generally found that the rock can be reduced to a smaller chip size thereby exposing up to double the surface area. For example, Hurst & Hewitt (1977 : 154) equated 2500 cm^2 with a 3·5 kg sample (i.e. >700 cm^2 per kg).

Although faunal density is a useful parameter which aids in the description of fossiliferous successions, values should be used with caution; for comparative purposes, only like or similar facies should be compared. It should also be noted that fossil remains at any given horizon not only represent the remains of the 'standing crop' or the living (biological) populations which inhabited that surface but also represent dead assemblages representing contemporary and earlier generations. However, since palaeoecologists can rarely distinguish between these categories effectively, density estimates refer simply to fossils in the rock and are not in any way precisely indicative of original population structures.

Identification and counting

All the fossils extracted from the rock by the 'crushing' process were identified and counted. The counting procedures outlined below are aimed at assessing the number of individual organisms in any sample. Different counting methods are required for the various fossil groups under consideration and produce varying degrees of accuracy. However, consistent methods are used for counting all representatives of any given group.

The Brachiopoda represent the most diverse and abundantly represented phylum encountered in this study. The number of individuals (N) per sample was estimated using the formula $N = A + \frac{1}{2}I + P$ (if $P > B$) or $A + \frac{1}{2}I + B$ (if $B > P$), where A, P, B and I represent the number of articulated pairs of valves, pedicle valves, brachial valves and indeterminate valves, respectively. The same method (with right and left being substituted for pedicle and brachial) was used to count the Bivalvia. This method has been used by other workers including Hurst (1975) and Watkins (1979). The numbers of individual gastropods, cephalopods, macheridians, tentaculitids and graptolites were counted singly.

Estimates of individual numbers in the five above-mentioned groups are far more accurate than for the other groups considered here. In assessing numbers of bryozoa it was assumed that a single complete colony could be regarded as an individual 'unit'. Since fragmentary remains do not generally outnumber complete or relatively complete specimens they too were regarded as each representative of a complete individual colony. Bryozoans were therefore also counted on a one to one basis; a significant overestimate of the abundance of colonies is considered no more probable than the likelihood of biased quantification in assessment of the numbers of other groups also to some extent represented by fragmentary remains.

The number of individuals represented by a collection of arthropod fossils is problematical since individuals may shed their exoskeleton many times during ontogeny (ecdysis). Ostracods almost invariably moult seven times before their ontogeny culminates in the eighth, maturation moult. Similar ontogenetic patterns are recorded in modern and fossil ostracods (Anderson 1964). In contrast, however, existing evidence on the ontogeny of various trilobite groups suggests considerable variation in the number of moults produced, for example between representatives of the Agnostina (Hunt 1967) and the Olenellinae (Raw 1927) or the Olenidae (Palmer 1957, Cisne 1973). Estimates of the number of instars produced during ontogeny range from 9 in the case of the agnostids to about 29 for the olenellids and olenids, with the majority considered representative of the adult (holaspid) stage. Variations in trilobite and ostracod moult patterns are reviewed in greater detail elsewhere (Lockley 1977).

A consideration of arthropod ecdysis favours the conclusion that a given number of trilobite or ostracod exoskeletons in any fossil assemblage is likely to represent fewer individual organisms.

For example, an ostracod could theoretically produce up to eight pairs of valves (albeit of differing sizes) whilst a trilobite could produce many exoskeletal moults, with up to 50% representing adult instars showing little or no significant size differences. With our present incomplete understanding of trilobile ecdysis, in addition to known variation amongst groups and complicating factors such as sexual dimorphism and fragmentation associated with ecdysis, any correction factor used to avoid overestimation of numbers is highly arbitrary. Nevertheless, various authors have estimated numbers of trilobites either without using any correction factor (e.g. Bayer 1967, Hurst 1975) or by dividing a total number of exoskeleton remains by a correction factor such as 10 (e.g. Pickerill 1974). This later example echoes the suggestion of Harrington *et al.* (1959 : 111) that less than 10% of trilobite remains are likely to belong to dead individuals. Either method tends to produce estimates approaching theoretical extreme values.

In this study correction factors of 8 and 4 were used for the Ostracoda and Trilobita respectively. Since all ostracod valves were counted without making a distinction between left and right, it was assumed that, ignoring the first instar (the egg), an individual could be represented by between 0 and 16 valves. A correction factor of 8 was therefore chosen as a mean estimate between theoretical minima and maxima. Similarly, it was assumed that if none of the trilobites encountered in this study were represented by more than eight holaspid instars then a mean correction factor would approximate to four. Corrected counts were therefore derived by estimating one individual for every four pygidia or cephala depending on which fragment was most numerous. Throughout the study fragments of pygidia or cephala for all species were generally found to be complete and representative of the holaspid stage. It could therefore be argued that the absence of a complete series of instars would call for a relatively low correction factor (i.e. less than 10) to avoid excessive underestimation. However, since the correction factors are acknowledged as arbitrary it is emphasized that the use of a correction constant does not obscure the original data.

In this study most of the crinoid remains recovered were fragmentary; it was therefore impossible to assess a representative number of individuals. Counts made of all ossicles and stem fragments are presented in the data tables where the presence of crinoid material is otherwise indicated simply by the addition of one to the total of individuals per sample.

Data synthesis and presentation

Having assessed the number of individuals in each taxon, totals for each sample were calculated; these totals accompany counts for each taxon and are presented in a series of tables which each represent one of the sampled sections.

The taxonomic level of classification employed in these tables, although variable, is essentially specific. In all but a few cases the generic names of Brachiopoda and Trilobita refer unequivocally to members of single-species populations as defined by Williams (1963) and Whittington (1962–68). Categories which do not necessarily represent only a single species population are as follows: Inarticulata, dalmanellid indet., Stroph. indet. and Trilobita indet. The remaining fauna is classified into the following series of generic or suprageneric groups: Mollusca or Bivalvia, Gastropoda (or *Sinuites* and *Cyclonema*), Cephalopoda, Macheridia, Monoplacophora, Tentaculites, Ostracoda (or *Tallinnella* and *Primitia*), Bryozoa indet. (or ramose bryozoa, '*Prasopora*' and cateniform bryozoa) and Crinoidea. These classifications generally represent one morphotype or morphospecies, although in certain cases categories such as Mollusca are used either to group minimal numbers of representatives of different molluscan taxa or to indicate uncertainty about the taxonomic affinities of particular specimens.

Where known species or genera are grouped within a broader classification (e.g. the Bivalvia, in Fig. 8, p. 179, are represented by *Modiolopsis*, *Cuneamya*, *Cyrtodonta* and others), full details are given at the appropriate point in the text.

All tabulated figures refer to original counts of specimens except in the case of the trilobites where numbers represent 25% of the maximum number of either pygidia or cephala following the rationalizations given above. Although ostracod numbers are assessed by a similar arbitrary method the original counts of valves are given (in brackets). Similarly, for Crinoidea counts of ossicles (in brackets) and stems [in square brackets] are also presented.

The totals of individuals per sample are tabulated and used as a basis for estimating the relative abundance (%) of the taxa at each horizon. Graphic representations of these distributions are presented in Figs 5 (p. 177), 11 (p. 182) and 16 (p. 189) where the percentage of taxa from all samples with over 20 individuals is plotted; those with less than 50 individuals are indicated by a dot to the left of the columns. A sample with at least 50 individuals is considered to reflect the composition (%) of the fauna at a given horizon adequately (Watkins 1975), whilst samples with 20-50 individuals, which characterize many less fossiliferous horizons, are invariably found to give consistent percentage values when compared with larger (> 50) samples. Although arbitrarily chosen, these minimum sample size figures ensure at least a consistent and minimum level of statistical constraint on data used for further extrapolation.

The size (weight) of each sample is indicated on most tables and can be used to assess faunal densities.

The total number of taxa in any sample is used as an estimate of the faunal diversity (or species richness) at any horizon. The diversity values presented here cannot necessarily be calculated from the tables since, in certain cases, the suprageneric taxonomic categories represent two or more taxa. In addition to the gross species richness (taxa per sample) presented here corrected, size-standardized diversity graphs are also given using the Margalef (1958) method and the Sanders (1968) rarefaction technique.

Trace fossils

Trace fossils in the Bala to Dinas Caradoc succession are neither common nor varied; for this reason they are not described in detail. However, a few examples are noted (Lockley 1977, 1980); Pickerill (1977) has outlined contemporary Caradoc trace faunas from the Berwyn region.

The faunal succession

The sections (numbered I–XII according to geographical location in Fig. 1, p. 168) are described here in a different sequence based on relative stratigraphical position. The description of these twelve sections is prefaced by the presentation of some additional information on the faunal composition of the Derfel Limestone, the basal member of the Lower Bala Group.

The Derfel Limestone

A large (10 kg) sample from the fossiliferous shelly shales representative of the Derfel Limestone at the type locality (SH 850395) was subjected to routine processing and analysis, to compare the composition of the fauna with that found in the younger Gelli-grîn Formation. Since Williams (1973) referred faunas from both stratigraphical levels to the *Nicolella* association, after having described the older fauna as a *Nicolella–Kullervo–Palaeostrophomena* association (Williams *in* Whittington & Williams 1955), both faunas were similarly analysed to establish points of comparison. The sample yielded specimens representative of at least 28 taxa, which are listed below in ranked order of abundance, with corrected numbers of individuals in brackets. Ramose bryozoans (35), *Dolerorthis* (28), *Platystrophia* (15), *Anisopleurella** (13), *Oxoplecia* (10), *Nicolella* (9), *Salopia* (9), Plectambonitacea indet. including *Sericoidea* and three other* listed genera (9), dendroid graptolite (9), *Onniella* (6), *Leptestiina** (4), prasoporid (4). *Howellites*, *Kullervo*, *Eoplectodonta**, *Leptaena*, *Deacybele* ? sp., *Broeggerolithus* (all 2). ? *Lingulella*, *Palaeostrophomena*, *Cyrtonotella*, Brachiopoda indet., *Platylichas*, Ostracoda, Macheridia, Crinoidea, Cystoidea, spicules (all 1). A total of 173 individuals is estimated from the above list.

Cyphoproetus is recorded in the Ordovician of Wales for the first time; similarly the occurrence of *Lingulella* is the first record of a representative of the Inarticulata in this member (Lockley 1980). The relative abundance of the brachiopods *Dolerorthis* and *Nicolella* compare with abundances noted in parts of the Gelli-grîn Formation, whilst the occurrence of *Platystrophia*, *Anisopleurella*, *Oxoplecia*, *Salopia*, *Onniella*, *Leptestiina*, *Sericoidea*, *Eoplectodonta* and *Palaeostrophomena* at both horizons is also noteworthy.

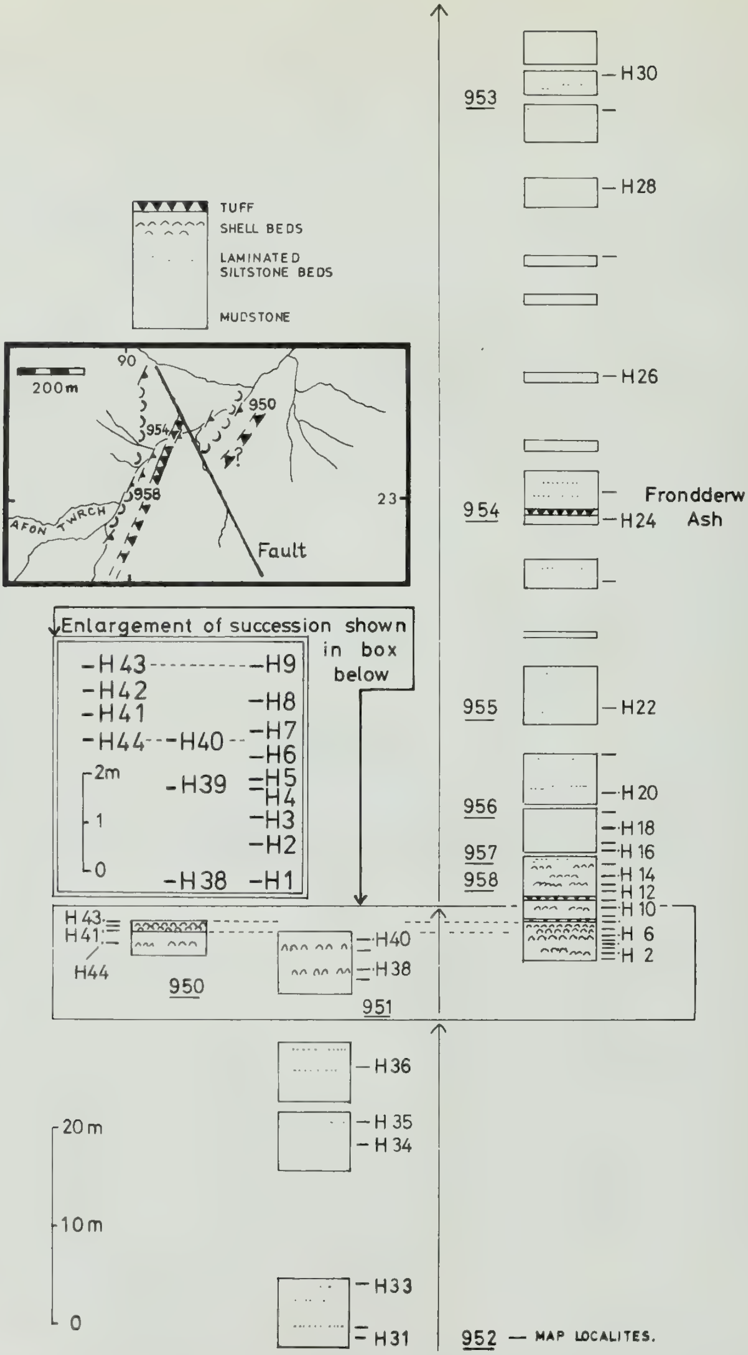

TUFF
SHELL BEDS
LAMINATED SILTSTONE BEDS
MUDSTONE
200m
90
950
954
958
23
AFON TWRCH
Fault
Enlargement of succession shown in box below
-H43----------H9
-H42
-H41
-H8
-H7
-H44---H40--
-H6
2m
-H39
-H5
-H4
1
-H3
-H2
0
-H38
-H1
953
H30
H28
H26
954
Frondderw Ash
H24
955
H22
956
H20
H18
957
H16
958
H14
H12
H10
H6
H2
H43
H41
H44
950
H40
H38
951
H36
20m
H35
H34
10m
H33
0
H31
952 — MAP LOCALITES.

Fig. 3 Sample points in the Afon Twrch section with inset map showing outcrop of sampled beds associated with shell beds and the Frondderw Ash in the upper reaches of Afon Twrch.

The Nant Hir Mudstones, Glyn Gower Siltstones and equivalent deposits

Although Bassett *et al.* (1966 : 229–230) listed faunas from various horizons in the Nant Hir Formation, no shelly fauna is known from the Nant Hir or the equivalent part of the Ceiswyn Mudstone at any locality south of northing 315. Similarly a large part of the overlying Glyn Gower Formation and equivalent beds to the south are only sparsely fossiliferous, with a low diversity fauna typified by the forms listed by Bassett *et al.* (1966 : 231). For this reason ambitious sampling schemes were not applied to sections through this part of the succession. However, near the headwaters of Afon Twrch an important series of fossiliferous beds is exposed in a section which contains a newly-discovered outcrop of the Frondderw Ash Member. The fauna, although dominated by *Heterorthis* and *Sowerbyella*, also contains elements previously considered as representative of the *Nicolella* association.

The Afon Twrch section and equivalent beds

The horizons sampled in this section are representative of the upper part of the Llaethnant Siltstone Formation (equivalent to the upper part of the Glyn Gower Formation) and the lower part of the Allt-Ddu Formation. Figs 3, 4 and 5 show respectively the field location and sample grid, faunal distribution and relative abundance patterns relating to this part of the succession. A series of 44 samples (total weight 232 kg) was collected from riverside exposures between map locs 950 (grid ref. 9133 2330) and 958 (9101 2305). However, in this section faulting (Lockley 1977, 1980) has caused duplication of part of the faunal succession (Figs 3, 5). Outcrops of *Heterorthis*-dominated shell beds are found in the repeated parts of the sequence and, since both outcrops are sampled at close vertical intervals, samples representative of beds thought to be precisely equivalent are bracketed together in Fig. 4.

There is a dual significance in the distribution of taxa recorded in the Twrch section. Firstly, the occurrence of *Heterorthis* (in abundance) at an horizon some 40 m below the Frondderw Member contrasts with the occurrence, elsewhere to the north, of *Heterorthis* assemblages in the Lower part of the Allt-Ddu Formation (see Bassett *et al.* 1966 : 234 and Fig. 6, p. 178).

A second noteworthy aspect of the distributions shown here is the occurrence of certain genera hitherto thought to be confined to the Gelli-grîn Formation and the Derfel Limestone Member. These include *Orthisocrania*, *Nicolella*, *Onniella*, *Salopia* and *Chasmops*. *Dolerorthis* is also recorded; although known from the Upper Allt Ddu Formation it is otherwise confined to the Derfel Limestone and the Gelli-grîn Formation. All these forms are characteristic of the *Nicolella* association and although, with the exception of *Onniella*, they are rare at this horizon, their occurrence can be considered indicative of the sustained establishment of this type of association, in this general area, through the Lower Caradoc. With the exception of *Dolerorthis* and *Chasmops*, representatives of the above-mentioned genera are figured in the taxonomic section.

When traced southwards to a gully on the north side of the Dyfi Valley (map and sample loc. 202, grid ref. 896217) beds equivalent to the Frondderw Member and the underlying shell beds are known (Lockley 1977, 1980). Fig. 5, which outlines the faunal distributions recorded at horizons in this part of the succession, indicates a significant lateral change in the composition of the shell bed beneath the Frondderw Ash. There is no evidence for the presence of *Heterorthis* and only the occurrence of *Onniella*, *Bicuspina* and the association of a minor ash are comparable with characteristics of the Twrch section. Since these shell beds are associated with thin parallel laminated, storm-generated siltstone sheets they are considered to represent transported material.

It is of particular interest to note that *Sowerbyella* and *Heterorthis* are almost entirely mutually exclusive though the two forms occur in abundance in beds separated by only a fraction of a metre (Fig. 5). J. M. Hurst (personal communication, 1978) has noted some degree of segregation between these two genera in the Alternata Limestone of Shropshire. It is possible that such patterns represent a differential response to the effects of transportation. Both forms have atrophied pedicles and would have therefore been relatively susceptible to disturbance by currents.

The Beudy Isaf and Ty-nant sections

Unlike the relatively remote Twrch and Dyfi sections, the Beudy Isaf and Ty-nant sections are

	wt	N	Inarticulata	Nicolella	Dolerorthis	Dinorthis	dalmanellid, indet	Howellites	Onniella	Reuschella	Heterorthis	Salopia	Bicuspina	Sowerbyella	Sericoidea	Leptaena	Macrocoelia	Brongniartella	isotelinid	Broeggerolithus	Gastropoda	Bivalvia	Cephalopoda	prasoporid	ramose bryozoa	Tallinnella		Crinoidea		
H 30	6	511	—	—	—	—	—	149	9	2	—	—	7	336	—	1	1	—	—	1	—	—	1	1	2	—	—	1	(35)	—
H 29	10	70	2	—	—	—	—	—	—	35	3	—	—	—	—	—	—	2	—	2	—	—	1	—	23	1	(7)	1	(234)	[5]
H 28	6	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H 27	4	43	2	—	—	—	—	10	—	3	—	—	—	21	—	—	—	1	—	1	—	—	—	—	3	1	(6)	1	(20)	[3]
H 26	8	8	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	2	1	(2)	1	(27)	—
H 25	5	13	—	—	—	—	—	2	—	3	—	—	—	—	—	—	—	—	—	1	—	—	—	1	5	—	—	1	(50)	[4]
H 24	6	15	—	—	—	—	—	2	—	2	—	—	—	—	—	—	—	1	—	—	—	—	—	—	9	—	—	1	(13)	[1]
H 23	2·5	5	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	(5)	—
H 22	4	11	—	—	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	1	(1)	1	(18)	[1]
H 21	6	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H 20	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	(3)	—
H 19	1·5	141	—	—	—	—	3	—	—	—	—	—	—	137	—	—	—	—	—	—	—	—	—	—	—	—	—	1	(8)	—
H 18	2	106	—	—	—	—	—	—	3	3	—	—	—	98	—	—	—	—	—	1	—	—	—	—	—	—	—	1	(20)	—
H 17	3	251	—	—	—	—	7	—	—	2	—	—	—	238	—	—	—	—	—	1	—	—	—	—	2	—	—	1	(28)	[2]
H 16	3	126	—	—	—	—	26	—	1	4	—	—	—	92	—	1	—	—	—	1	—	—	—	—	—	—	—	1	(27)	—
H 15	6	259	—	—	—	—	7	—	—	3	236	—	3	—	1	—	—	1	—	2	2	—	—	—	2	1	(11)	1	(20)	—
H 14	7·5	285	—	—	—	—	14	—	—	—	241	—	1	5	—	—	—	1	—	7	2	1	1	8	—	3	(25)	1	(1)	[1]
H 13	6	169	2	—	—	—	5	—	—	5	122	—	7	5	—	—	—	—	—	3	4	1	1	4	7	2	(17)	1	(238)	[5]
H 12	5·5	211	4	—	2	2	13	—	—	8	141	—	22	1	—	1	—	—	—	1	1	1	3	5	4	1	(5)	1	(79)	—
H 11	6·5	199	1	—	—	2	14	—	—	13	125	1	12	—	—	—	—	1	—	2	—	—	1	12	13	1	(7)	1	(47)	—
H 10	5·5	362	4	—	—	—	12	—	—	10	282	—	18	—	—	1	—	—	—	2	—	1	4	16	10	1	(6)	1	(27)	—
H 9	3·5	99	1	—	—	—	6	—	1	12	52	—	5	—	—	1	—	—	—	4	—	—	—	5	10	1	(10)	1	(31)	—
H43	6	176	1	—	—	—	12	—	—	13	127	—	8	1	—	—	—	1	—	1	2	—	2	4	2	1	(4)	1	(40)	—
H42	4	203	2	—	—	—	3	—	—	4	167	—	10	—	—	—	—	—	—	2	—	—	2	5	6	1	(1)	1	(11)	—
H 8	2·5	85	2	—	—	4	2	2	4	10	48	—	3	1	—	—	—	—	—	2	—	—	2	—	3	1	(2)	1	(16)	—
H41	4·5	141	1	—	—	2	—	—	9	8	115	—	—	1	—	—	—	—	—	1	—	—	—	1	1	1	(4)	1	(8)	—
H 7	4·5	210	2	—	—	1	27	7	25	86	5	—	19	2	—	1	—	—	—	2	—	—	1	11	16	4	(30)	1	(25)	—
H40	10	213	—	3	—	10	—	—	31	35	—	—	6	103	—	—	—	2	1	2	3	—	5	11	—	—	—	1	(53)	—
H44	1·5	67	—	—	—	1	10	—	—	38	3	—	7	—	—	—	—	—	1	1	—	—	—	2	2	1	(3)	1	(23)	—
H 6	5·5	365	1	2	—	4	13	2	35	52	—	1	15	214	—	—	—	1	1	1	—	—	1	8	12	1	(1)	1	(47)	—
H 5	6	400	2	—	—	—	2	66	62	4	—	—	10	247	—	—	—	1	—	1	—	—	—	2	1	1	(3)	1	(14)	[1]
H39	6	109	—	—	—	—	3	—	—	1	—	—	4	89	1	—	—	1	—	1	—	—	—	6	2	—	—	1	(67)	[3]
H 4	8	385	1	—	—	—	4	43	81	8	—	—	9	226	—	1	—	1	—	2	—	—	—	7	—	1	(5)	1	(129)	—
H 3	4	19	1	—	—	—	3	—	—	3	—	—	1	7	—	—	—	1	—	1	—	—	—	—	1	—	—	1	(15)	—
H 2	6	50	1	—	—	—	4	—	—	13	—	—	—	29	—	—	1	—	—	1	—	—	—	—	—	—	—	1	(7)	—
H 1	6·5	29	—	—	—	1	3	—	1	12	—	—	—	—	—	—	—	1	—	1	1	—	—	1	6	1	(6)	1	(31)	[1]
H38	6·5	306	1	—	1	1	48	12	79	85	5	1	12	45	—	—	—	1	1	3	1	—	—	8	—	1	(10)	1	(73)	[2]
H37	6	53	2	—	—	—	7	—	—	12	3	—	—	—	—	—	—	2	—	1	—	—	—	—	24	1	(4)	1	(200)	[1]
H36	6	24	2	—	—	—	11	—	—	—	—	—	—	2	—	—	—	2	—	1	1	—	—	—	4	1	(7)	1	(17)	[6]
H35	4·5	47	4	—	—	—	—	33	—	1	1	—	—	—	—	—	—	1	—	1	—	—	—	—	3	2	(12)	1	(18)	[1]
H34	5	22	—	—	—	—	—	14	—	—	—	—	—	2	—	—	—	1	—	1	—	—	—	—	2	1	(1)	1	(1)	—
H 33	5·5	11	—	—	—	—	—	2	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	1	(5)	(4)
H 32	6	13	—	—	—	1	—	1	—	4	—	—	—	—	—	—	—	1	—	—	—	—	—	2	2	1	(1)	1	(32)	[3]
H 31	6	7	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	2	1	(1)	1	(41)	—

Fig. 4 Fauna from the Afon Twrch section.

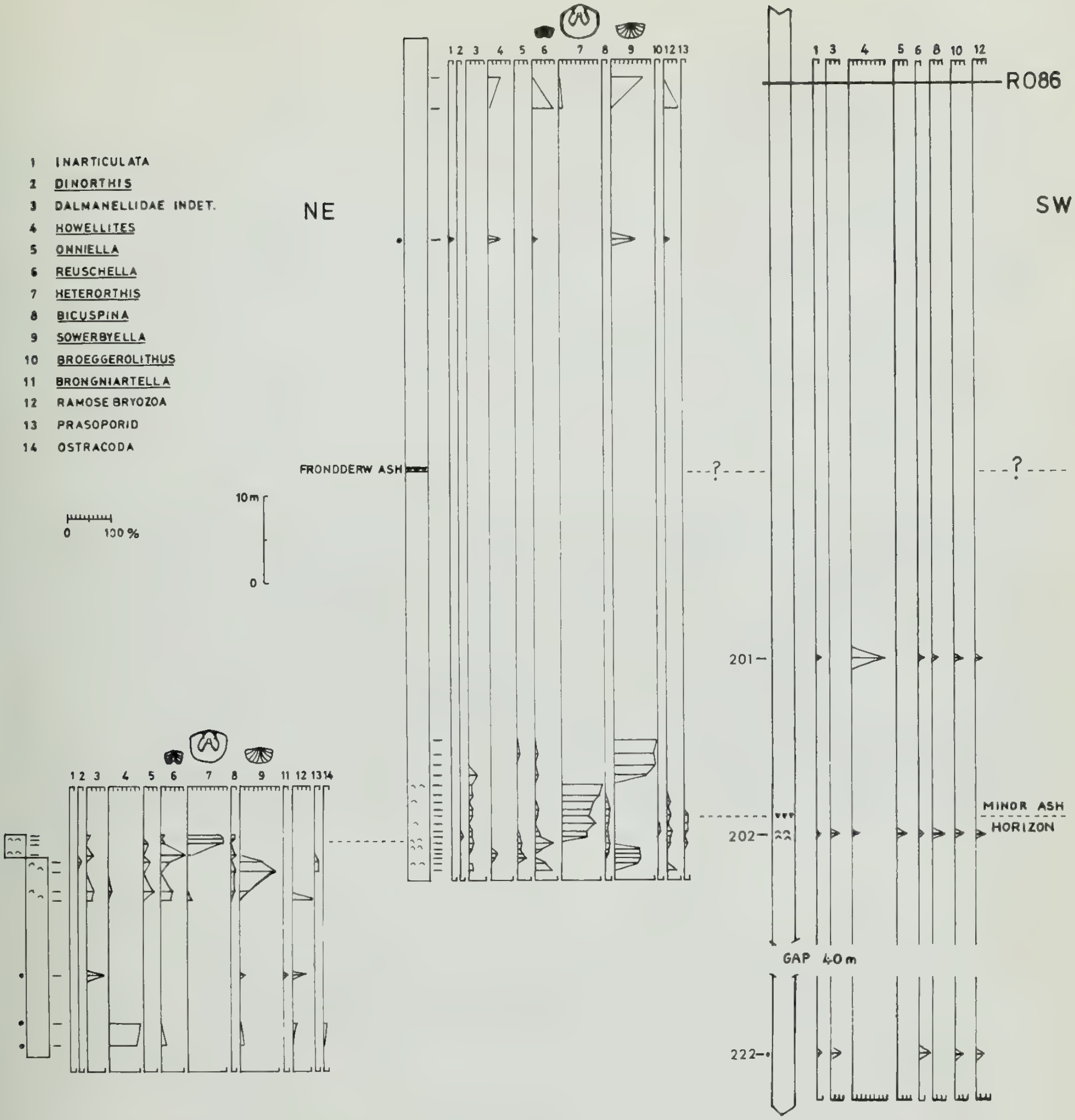

1 INARTICULATA
2 DINORTHIS
3 DALMANELLIDAE INDET.
4 HOWELLITES
5 ONNIELLA
6 REUSCHELLA
7 HETERORTHIS
8 BICUSPINA
9 SOWERBYELLA
10 BROEGGEROLITHUS
11 BRONGNIARTELLA
12 RAMOSE BRYOZOA
13 PRASOPORID
14 OSTRACODA
0 100 %
10m
0
NE
SW
R086
FRONDDERW ASH
?
MINOR ASH HORIZON
201
202
222
GAP 40 m
1 2 3 4 5 6 7 8 9 10 12 13
1 2 3 4 5 6 7 8 9 11 12 13 14
1 3 4 5 6 8 10 12

Fig. 5 Sample points in Afon Twrch section (NE) and the lower part of the Dyfi Valley section (SW) below lowest upper Allt Ddu sample (R086). Dotted lines indicated inferred correlations.

accessible by road. Fig. 6B shows the composition of faunas collected from six stratigraphically sequential horizons in the small stream gully east of Beudy Isaf (9105 2495). The section covers some 20 m of beds, passing upward from the gully to fossiliferous roadside exposures (9115 2505) containing numerous *Heterorthis* specimens. This section represents a part of the lower to middle Allt Ddu Mudstone (Fig. 1, p. 168) and is not therefore contemporary with the deposit found in the upper reaches of Afon Twrch. *Sowerbyella* and *Heterorthis* are again found to be mutually exclusive.

The Ty-nant section (Fig. 6A) is represented by a series of widely-spaced samples recovered from the Nant Bwlch-y-pawl valley east of Ty-nant (9050 2625). The Frondderw Ash exposed

LOCALITY	TOTAL	*Paracraniops*	*Dalmanellidae*	*Reuschella*	*Heterorthis*	*Bicuspina*	*Sowerbyella*	stroph. indet.	*Broeggerolithus*	nuculid	Gastropoda	Bryozoa	Ostracoda	Crinoidea	Graptoloidea	DIVERSITY
A																
35	18	1	9	-	-	-	-	-	1	1	-	-	1(3)	-	5	6
9	36	-	4	5	22	-	-	2	1	-	-	1	-	1(10)	-	7
6	66	-	9	-	47	1	-	2	1	-	-	4	1(2)	1(69)	-	8
2	4	-	-	1	-	-	-	-	-	-	-	2	-	1(1)	-	(3)
1022B	2	-	-	1	-	-	-	-	-	-	-	-	-	1(6)	-	(2)
1022	-	x x x x x x x x x FRONDDERW ASH x x x x x x x x														x
1022A	103	-	1	1	-	-	99	1	-	-	-	-	-	1(14)	-	5
B																
790B	61	1	4	12	37	4	-	-	1	-	-	1	-	1(13)	-	8
790A	66	1	3	1	56	1	-	-	1	-	-	2	-	1(65)	-	8
790	27	-	2	-	-	-	24	-	-	-	-	-	1	-	-	(3)
789	13	-	9	-	-	-	-	-	1	-	3	-	-	-	-	(3)
997B	38	-	2	-	-	-	33	-	1	-	-	1	1	1(10)	-	5
997A	13	-	-	12	-	-	-	-	-	-	-	-	-	1(1)	-	(2)

Fig. 6 Fauna from the Ty Nant section (A) and the Beudy Isaf section (B).

under the bridge in the farmyard succeeds mudstones with *Sowerbyella* shell beds and is overlain by massive siltstones with a sparse fauna. Outcrops higher in the succession at streamside locs 400 m and 700 m east of the farm yield a *Heterorthis*-dominated fauna similar to that recorded in the upper part of the Beudy Isaf section. Loc. 35 (9167 2665) yielded a typical middle to upper Allt Ddu fauna characterized by the presence of graptolites and a nuculid bivalve (Fig. 96, p. 225). Immediately to the north of this locality and higher in the succession on the ridge known as Pen-y-Cefn-Coch two outcrops of upper Gelli-grîn beds were discovered. These yielded a fauna dominated by bryozoa, *Leptestiina*, *Dolerorthis* and *Skenidioides* and containing characteristic elements like *Estoniops*, *Nicolella* and *Rhactorthis* (Fig. 7A). Outcrops at loc. 615 (9150 2685) consist mainly of well-bedded limestones typical of the Cymerig Member, whereas at loc. 615A (9170 2700) a coarse tuffaceous, calcarenite lithology is indicative of beds immediately above the limestone member. The recognition of precise stratigraphical relationships is hampered by poor exposure and local faulting (Lockley 1977, 1980).

LOCALITY	TOTAL	*Paracraniops*	*Nicolella*	*Dolerorthis*	*Rhactorthis*	*Skenidioides*	*Platystrophia*	*Dalmanella*	*Howellites*	*Onniella*	dalmanellid, indet.	*Reuschella*	*Bicuspina*	*Eoplectodonta*	*Leptestiina*	*Sericoidea*	*Leptaena*	stroph. indet.	*Cyclospira*	*Platylichas*	*Estoniops*	isotelinid	*Kloucekia*	*Flexicalymene*	*Brongniartella*	*Broeggerolithus*	Cephalopoda	Conularida	tentaculite	ramose bryozoa	prasoporid	Ostracoda	Crinoidea	DIVERSITY
A																																		
615A	109	-	4	10	4	11	1	-	-	-	9	1	-	-	9	3	2	6	3	1	1	-	-	-	-	-	-	1	6	13	13	-	1(10)(2)	28
615	28	-	1	-	-	-	-	-	-	-	4	-	-	-	6	1	-	-	-	-	-	1	-	-	-	-	-	-	-	12	2	-	1(110)(3)	8
B																																		
555B	366	-	3	6	1	4	-	-	245	-	7	1	-	7	-	-	2	3	-	-	-	-	2	2	-	18	-	-	-	46	17	1(9)	1(5)	17
555A	188	-	-	-	1	3	-	-	63	-	29	-	3	12	1	-	1	1	-	-	-	-	3	3	2	9	1	-	1	38	14	2(19)	1(8)(2)	19
		(Stratigraphical gap of 35 m)																																
557	419	1	4	-	-	1	-	39	18	-	35	1	10	230	15	-	1	7	-	-	-	-	1	2	1	7	-	-	-	35	7	3(23)	1(30)	19

Fig. 7 Fauna from Pen y Cefn Coch (A) and Lledwyn Bach (B). (For Conularida read Macheridia.)

The Allt Ddu Formation at Craig y Gath and Rhiw March

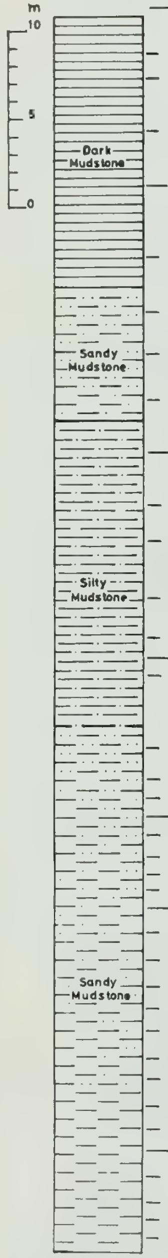
Figs 8 and 9 show the distribution of faunas in the upper part of the Allt Ddu Formation at Craig y Gath and Rhiw March respectively and Fig. 11 shows percentage abundances.

Bassett *et al.* (1966 : 235) stated that the Allt Ddu succession 'is best seen at Craig y Gath (915306)' and pointed out that, in addition to considerable repetition caused by faulting at the type locality, the junctions with neither the underlying nor with the overlying member are seen in this area. For this reason Craig y Gath is regarded here as the alternative type section.

	wt	N	Paracraniops	Cinorthis	Skenidioides	Onniella	Howellites	Reuschella	Bicuspina	Sowerbyella	Eoplectodonta	Macrocoelia	Leptaena	Rostricellula	Flexicalymene	Brongniartella	Broeggerolithus	isotelinid	Gastropoda	Bivalvia	Cephalopoda	ramose bryozoa	prasoporid	Conularida	Ostracoda		Crinoidea			Graptoloidea
AD Z	4	50	—	—	—	9	—	1	1	—	18	1	1	—	—	—	1	—	—	—	—	3	10	3	1	(9)	1	(76)	—	—
AD Y	5	193	3	1	5	46	—	8	2	—	76	1	6	—	2	1	1	—	—	—	—	8	17	13	2	(13)	1	(243)	—	—
AD X	6	51	5	—	—	—	13	14	—	—	—	3	—	1	—	2	2	—	—	1	1	1	1	3	2	(18)	1	(18)	[1]	1
AD W	7	83	10	6	—	—	37	9	—	—	—	3	—	1	—	1	3	—	—	—	—	3	8	—	2	(15)	—	—	—	—
AD V	7	26	5	—	—	—	10	—	—	—	—	1	1	—	1	1	1	—	—	2	—	—	1	1	1	(5)	1	(1)	—	—
AD U	6	217	3	7	—	—	59	13	7	86	—	13	4	1	—	1	2	—	1	—	—	3	14	2	—	—	1	(34)	—	—
AD T	6	51	18	2	—	—	22	—	—	—	—	1	2	1	1	—	1	—	—	—	—	—	1	—	1	(5)	1	(22)	—	—
AD S	7	35	11	—	—	—	8	—	—	2	—	7	—	—	1	1	2	—	—	—	—	—	1	—	1	(8)	1	(5)	—	—
AD R	7	32	2	—	—	—	18	3	—	—	—	1	—	2	—	—	1	1	1	—	—	2	—	—	—	—	1	(24)	[1]	—
AD Q	7	15	—	—	—	—	12	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	1	(8)	—	—
AD 3 L	—	57	10	—	—	—	30	—	—	—	—	2	—	—	—	—	6	—	—	1	2	1	4	—	—	—	1	(8)	—	—
AD P	8	91	1	—	—	—	73	—	—	—	—	1	—	—	—	1	5	—	1	—	—	6	2	—	—	—	1	(1)	—	—
AD O	9	179	7	—	—	—	144	—	—	—	—	—	—	—	—	1	3	—	9	1	—	14	—	—	—	—	—	—	—	—
AD N	4	26	1	—	—	—	23	—	—	—	—	—	—	—	—		1	—	—	—	—	1	—	—	—	—	—	—	—	—
AD M	4	6	1	—	—	—	4	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
AD L	4	18	2	—	—	—	13	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	1
AD 3 J	—	246	4	—	—	—	201	—	2	—	—	7	—	—	—	1	9	1	1	4	1	—	14	—	—	—	1	(15)	[1]	—
AD K	4	9	2	—	—	—	3	—	—	—	—	—	—	—	—	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—
AD J	5	3	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	(1)	—	—	—	—
AD I	6	5	—	—	—	—	—	—	—	—	—	—	—	2	—	1	1	—	—	—	—	—	—	—	1	(2)	—	—	—	—
AD H	5	2	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
AD G	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	(2)	—	—	—	—
AD F	5	10	1	—	—	—	5	—	—	—	—	—	—	—	—	—	1	—	—	1	—	1	—	—	1	(1)	—	—	—	—
AD E	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	(1)	—	—	—	—
AD D	4	3	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—
AD C	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
AD B	5	22	5	—	—	—	4	—	—	1	—	—	—	—	—	—	2	—	—	4	1	—	—	—	1	(5)	1	(1)	—	3
AD A	7	17	3	—	—	—	3	—	—	—	—	1	—	—	—	1	2	—	—	4	—	—	—	—	1	(1)	1	(1)	—	1
AD 3 H	—	97	16	1	—	—	53	—	—	—	—	6	—	—	—	—	5	1	2	4	2	2	3	—	1	(7)	1	(12)	—	—
AD 3 G	—	16	6	—	—	—	5	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	1	(1)	1	(4)	[12]	—
AD 3 F	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
CYG 6	3	80	11	—	—	—	58	—	—	7	—	—	—	—	—	1	2	—	—	—	—	1	—	—	—	—	—	—	—	—
CYG 5	3	46	5	—	—	—	25	—	—	10	—	—	—	—	—	—	1	—	—	5	—	—	—	—	—	—	—	—	—	—
CYG 4	—	5	—	—	—	—	4	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
AD 3 C	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—

Fig. 8 Fauna from the Craig y Gath section. (For Conularida read Macheridia.)

The sample grid (covering 150 m of the succession) and a locality map are shown in Fig. 10. The two uppermost samples, recovered from the base of the Gelli-grîn Formation, yield a characteristic fauna dominated by *Onniella* and *Eoplectodonta*. However, the distribution of upper Allt Ddu faunas, both here and at Rhiw March, is characterized by an association of mainly long-ranging forms, all of which maintain a relatively consistent pattern of relative abundance throughout the succession. The fauna is dominated by *Howellites*, *Paracraniops*, *Macrocoelia* and *Broeggerolithus*.



			Paracraniops	dalm. indet.	Dalmanella	Howellites ult.	Onniella	Reuschella	Bicuspina	Sowerbyella	Sericoidea	Macrocoelia	Leptaena	Kiaeromena	Rostricellula	Flexicalymene	Brongniartella	isotelinid	Broeggerolithus	Trilobita, ind.	Bellerophon	Cyclonema	Bivalvia	Cephalopoda	Conularida	ramose bryozoa	Prasopora	bryozoa, indet.	cateniform br.	Tallinnella		Crinoidea		
	4·5	18	1	7	—	—	—	—	—	—	2	—	—	—	—	—	1	—	1	1	—	—	—	—	—	—	—	1	—	3	(25)	1	(2)	—
	4·5	6	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	2	(16)	—	—	—
	5	15	—	7	—	—	—	—	—	—	1	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	5	(37)	—	—	—
R20	6	32	3	3	—	—	—	—	—	—	4	—	—	—	—	—	1	—	2	—	—	—	—	—	—	—	—	—	—	19	(150)	—	—	—
	4	7	2	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	2	(16)	—	—	—
	7	263	—	—	1	134	5	—	7	53	10	—	4	—	—	—	2	—	2	1	—	—	—	—	15	—	24	—	—	4	(31)	1	(16)	[1]
	5	47	2	—	—	20	2	—	8	—	—	—	—	—	—	1	1	1	2	—	3	—	—	—	3	1	2	—	—	1	(2)	1	(53)	[4]
	7·5	43	9	—	—	4	—	—	5	—	—	1	4	—	—	1	1	—	2	—	2	—	—	1	2	4	2	—	—	4	(29)	1	(12)	[13]
15	6	24	2	—	—	9	—	—	—	—	—	1	—	—	1	1	1	—	3	—	—	—	1	—	—	3	—	—	—	1	(6)	1	(12)	—
	8	19	5	—	—	4	—	—	—	—	—	—	—	—	—	—	1	—	3	1	1	—	—	—	—	1	1	—	—	1	(9)	1*	—	—
	5·5	33	2	—	—	8	—	—	2	—	—	—	—	—	—	—	—	—	2	—	—	10	—	—	—	7	—	—	—	1	(1)	1	(12)	[2]
	6	22	4	—	—	10	—	—	—	—	—	—	—	—	—	—	—	—	2	1	1	—	—	—	—	2	—	—	—	1	(3)	1	(14)	[3]
	4·5	27	—	—	—	18	—	—	—	—	—	—	—	—	—	—	1	—	2	—	—	—	—	—	1	4	—	—	—	—	—	1	(15)	[1]
10	5	20	—	—	—	16	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	1	(2)	—	—	—
	3	5	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	1	(1)	1	(1)	—
	3·5	58	7	—	—	33	—	—	—	—	—	—	—	1	1	—	1	—	2	—	—	1	2	—	—	8	—	—	—	1	(1)	1	(25)	—
	4	29	—	—	—	10	—	4	5	—	—	—	—	—	—	1	1	—	2	—	—	1	—	—	—	3	1	—	—	—	—	1	(27)	—
	5·5	37	2	—	—	25	—	—	1	—	—	—	—	—	—	—	1	—	4	—	1	—	—	—	—	1	—	—	—	1	(6)	1	(85)	[16]
5	7	35	3	—	—	18	—	—	—	—	—	—	—	—	—	—	1	—	6	—	—	—	1	1	1	2	—	—	—	1	(5)	1	(8)	[2]
	3	9	1	—	—	2	—	—	—	—	—	1	—	—	—	—	—	—	3	—	—	—	—	—	—	1	—	—	—	—	—	1	(7)	[4]
	4	11	—	—	—	2	—	—	—	—	—	—	—	2	—	—	—	—	1	—	—	—	—	—	—	3	2	—	—	—	—	1	(16)	[1]
	6	71	2	—	—	37	—	—	3	—	7	—	2	—	—	—	1	—	4	—	—	2	—	—	4	5	2	—	—	1	(5)	1	(195)	[5]
	7	39	—	—	1	9	—	3	5	—	5	—	—	—	—	—	1	—	4	—	2	1	—	1	—	3	2	—	—	—	—	1	(28)	[2]
0	8	111	3	—	2	9	—	6	20	—	7	11	—	3	—	2	1	—	3	—	—	3	—	1	3	10	25	—	—	1	(3)	1	(125)	[10]
	7·5	44	—	—	—	5	—	3	6	—	1	3	5	—	—	—	1	—	1	—	1	1	1	—	—	10	5	—	—	—	—	1	(45)	[4]
	5·5	148	—	—	3	38	2	1	9	—	3	3	10	3	—	1	1	—	9	—	1	3	1	2	7	38	11	—	—	1	(1)	1	(105)	[10]
	6·5	25	3	—	—	—	—	—	—	—	1	—	—	—	1	—	2	—	10	—	—	—	—	1	—	4	1	—	—	1	(6)	1	(10)	—
	7·5	62	13	—	—	6	—	—	2	—	8	1	1	—	2	—	1	—	7	—	1	—	1	2	—	14	1	—	—	1	(2)	1	(18)	[2]
095	5·5	13	2	—	—	—	—	—	1	1	—	1	1	—	—	—	—	—	3	—	—	—	—	—	—	1	1	—	—	1	(2)	1	(11)	—
	2·5	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	7·5	103	32	—	4	35	—	—	—	—	3	3	1	—	1	1	2	—	11	—	1	—	1	—	—	2	—	4	—	1	(7)	1	(27)	[1]
	5	13	2	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	5	—	—	—	1	1	—	—	—	1	—	1	(6)	1	(3)	[1]
	4·5	15	3	—	—	1	—	—	—	—	1	—	—	—	1	—	1	—	5	—	—	—	—	—	—	—	1	1	—	1	(1)	—	—	—
090	6·5	45	1	—	—	30	—	—	1	—	—	3	—	—	—	—	1	—	2	—	1	—	1	—	—	1	1	—	1	1	(1)	1	(16)	—
	5	34	1	—	—	21	—	—	—	—	3	—	—	—	—	—	1	—	2	—	—	—	—	—	—	3	—	—	—	—	—	1	(3)	—
	6	128	4	—	2	77	3	—	3	—	7	—	1	—	—	1	1	—	6	—	—	2	—	—	—	6	10	—	1	1	(3)	1	(50)	[3]
	4·5	16	2	—	—	4	—	—	—	—	2	—	—	—	—	—	1	—	2	—	—	—	—	1	—	—	—	2	—	1	(2)	1	(6)	—
	5	11	—	—	—	6	—	—	—	—	1	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	1	(1)	—	—	—

Fig. 9 Fauna from the Rhiw March section (Allt Ddu beds). (For *Bellerophon* read *Sinuites*, and for Conularida read Macheridia.)

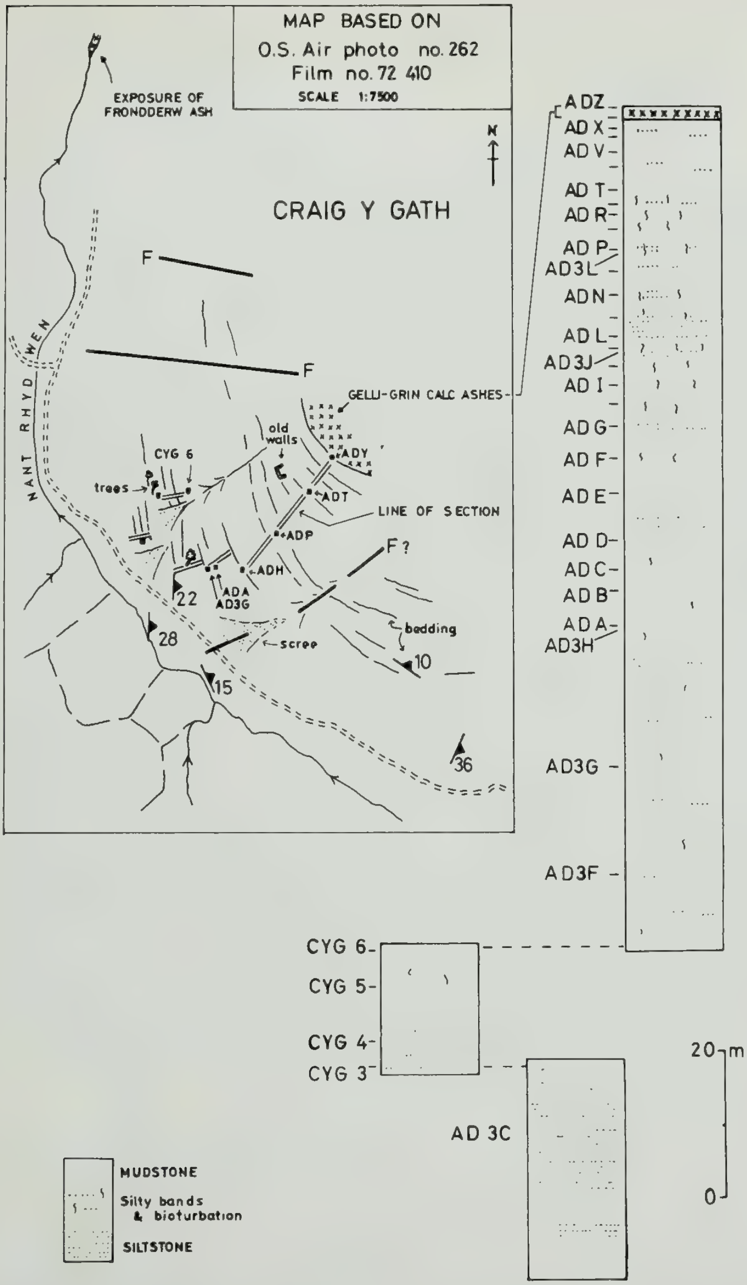

MAP BASED ON
O.S. Air photo no. 262
Film no. 72 410
SCALE 1:7500
EXPOSURE OF FRONDDERW ASH
N
CRAIG Y GATH
F
F
NANT RHYD WEN
GELLI-GRIN CALC ASHES
old walls
CYG 6
trees
ADY
ADT
LINE OF SECTION
ADP
F ?
ADH
ADA
AD3G
22
28
scree
bedding
10
15
36
ADZ
AD X
AD V
AD T
AD R
AD P
AD3L
AD N
AD L
AD3J
AD I
AD G
AD F
AD E
AD D
AD C
AD B
AD A
AD3H
AD3G
AD3F
CYG 6
CYG 5
CYG 4
CYG 3
AD 3C
20 m
0
MUDSTONE
Silty bands & bioturbation
SILTSTONE

Fig. 10 Map of Craig y Gath exposures showing sample points and their stratigraphical relationships.

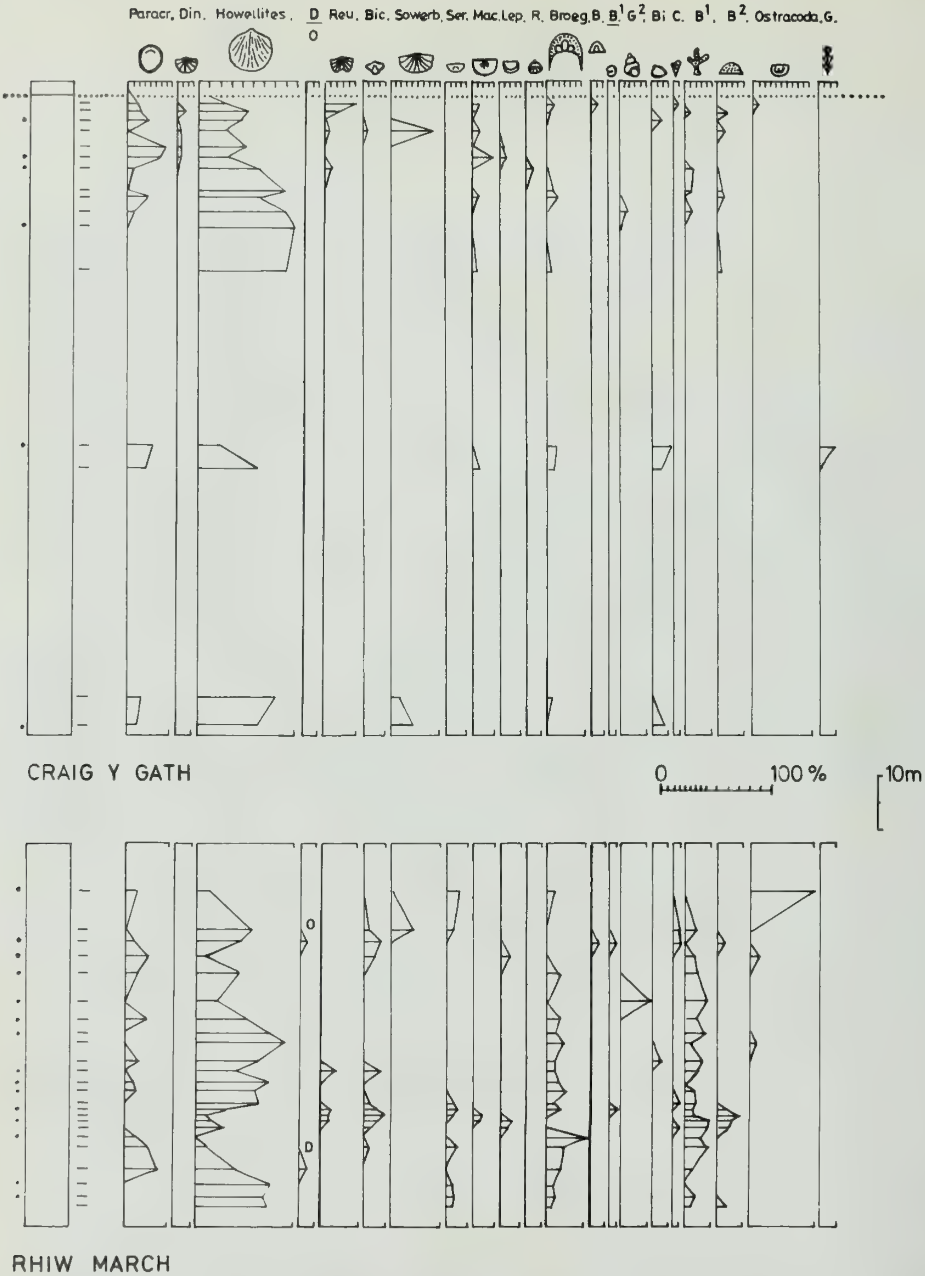


Fig. 11 Percentage distribution of taxa in the upper part of the Allt Ddu Formation at Craig y Gath and Rhiw March. Abbreviations refer to *Paracraniops* (Paracr), *Dinorthis* (Din), *Dalmanella* (D), *Onniella* (O), *Reuschella* (Reu), *Bicuspina* (Bic), *Sowerbyella* (Sowerb), *Sericoidea* (Ser), *Macrocoelia* (Mac), *Leptaena* (Lep), *Rostricellula* (R), *Broeggerolithus* (Broeg), *Brongniartella* (B), *Sinuites* (B¹), Gastropoda (G²), Bivalvia (Bi), Macheridia (C), ramose Bryozoa (B¹), prasoporid Bryozoa (B²), Graptoloidea (G). Lithostratigraphical boundary shown by dotted line.

Paracraniops (*P. glaber* sp. nov., Figs 33–36, p. 207) is an important element throughout the Allt Ddu and is even known from upper Glyn Gower and Llaethnant horizons. This form was previously unrecorded by workers in this area (e.g. Bassett *et al.* 1966), who ignored it because of uncertainty about its taxonomic affinity (A. Williams, personal communication, 1976). However, in the Caradoc successions of the Berwyn Hills to the east, Pickerill & Brenchley (1979) have described *Paracraniops* as an important element in the *Howellites* community. As demonstrated below their observations allow useful comparisons to be made between the composition of related faunal associations.

According to Bassett *et al.* (1966) and Whittington (1968) *Flexicalymene* was unknown in the upper part of the Allt Ddu Formation, but it has now been found at several horizons (Figs 8, 9).

Differences in the upper Allt Ddu faunal succession between Craig y Gath and Rhiw March are only pronounced with respect to particular taxa. For example, *Dinorthis*, which is confined to the uppermost part of the Craig y Gath succession, is unknown at Rhiw March, and *Sericoidea*, which is commonly found in the Rhiw March succession, is unknown at Craig y Gath and at other Allt Ddu localities north of Ty-nant.

The assemblage zones outlined by Bassett *et al.* (1966 : 236) are only entirely valid for the area they mapped (1966 : pl. 2). Although the lower, middle and upper Allt-Ddu assemblages (represented respectively by the *Heterorthis* faunule, a zone of faunal depletion and a zone characterized by 'new' stocks) can be recognized, where exposed, as far south as the Ty-nant area – with the possible exception of the upper zone – it is impossible to recognize these divisions within the formation in the Rhiw March section. For example, the zone of faunal depletion noted at Craig y Gath is not characteristic of equivalent horizons in the Rhiw March section (Fig. 2, p. 170). With respect to this zone it is of interest that these argillaceous beds, both at Craig y Gath and other localities (e.g. loc. 35, Fig. 6), are characterized by the presence of graptolites and small nuculoid bivalves.

Characteristic 'bursts' of *Sowerbyella* noted by Bancroft (1945) and Bassett *et al.* (1966 : 236) are apparently widespread in space but, in the upper part of the formation, restricted in time to only a few horizons. A *Sowerbyella* shell carpet or 'burst' occurs at about 8 m below the base of the Gelli-grîn Formation at Craig y Gath, and at about 16 m below the base at Rhiw March (samples ADU and R18). The likelihood of these two horizons, at localities 7 km apart, being contemporaneous is strongly supported by the occurrence of an unusually high concentration of archaeogastropods at an horizon exactly 14 m below the *Sowerbyella* 'burst' in both sections (samples ADO and R13). It is suggested that the widespread occurrence of abundant gastropod and *Sowerbyella* specimens at particular horizons could be indicative of a large successful spatfall or conditions otherwise conducive to the temporary proliferation of such specific groups.

The uppermost 30 m of the Allt Ddu Formation at Rhiw March are apparently equivalent to only 22 m of beds at Craig y Gath, where erosion before the deposition of the Gelli-grîn could have removed some 8 m of uppermost Allt Ddu deposits. Since respective lithologies for these uppermost beds are well-bedded silty mudstones and fine-grained argillaceous mudstones it is probable that reworking took place in the north while continuous deposition prevailed in the south.

Sampled sections through the Gelli-grîn Formation

Dominant faunal elements. Although only 60 m in thickness, the Gelli-grîn Formation represents the most lithologically varied, fossiliferous, and faunally diverse, stratigraphical unit in the Lower Bala Group; for this reason it has been examined here in particular detail. The formation crops out between Pont y Ceunant (SH 944346, about 1 km north of the type locality west of Gelli-grîn farm) and the Rhiw March section in the Dyfi Valley. To the south of this latter locality the formation passes laterally into argillaceous beds representative of the upper part of the Ceiswyn Mudstone and the overlying Nod Glas Formation. The distribution of faunas in five sections through the formation is shown in Figs 7B, p. 178, and 12–15. The chosen sections are at the following localities: west of Gelli-grîn farm, 944340 (Fig. 12), Maes-Meillion, 925305 (Fig. 13, p. 185), Lledwyn Bach, 912279 (Fig. 7B), Nant Tan y Bwlch, 914240 (Fig. 14, p. 186) and the

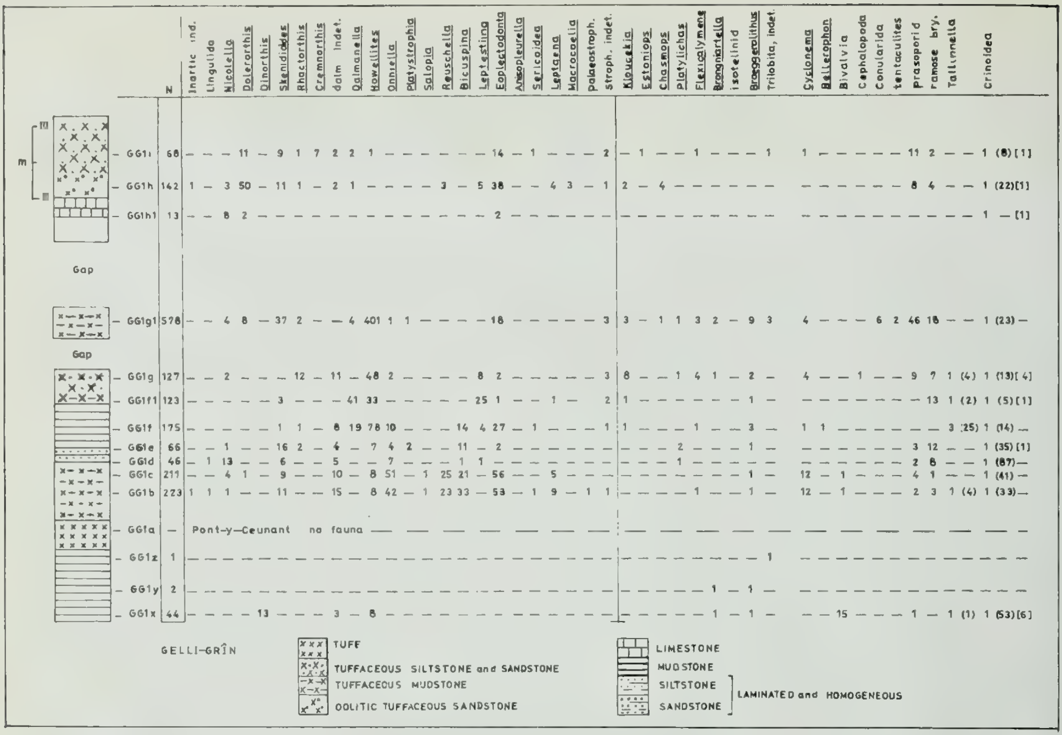


Fig. 12 Fauna from the Gelli-grîn (type) section. (For *Bellerophon* read *Sinuites*, and for Conularida read Macheridia.)

cliffs north of Rhiw March, 899219 (Fig. 15, p. 187). All sections, with the exception of the poorly-exposed outcrops at Lledwyn Bach, have been sampled thoroughly throughout.

In the Tan y Bwlch and Rhiw March sections the uppermost 20 m of beds not only belong to the Gelli-grîn Formation, but also represent the northern part of the outcrop of the Nod Glas Formation now known to be equivalent to this upper part of the Gelli-grîn Formation (Lockley 1977, 1980). The relative abundance of faunas in the four main Gelli-grîn sections is shown in Fig. 16, p. 189.

At the type locality a series of 15 samples was collected. Here the underlying uppermost Allt Ddu beds, where fossiliferous, contain a fauna dominated by *Dinorthis*, *Howellites* and bivalves. The succeeding coarse Pont y Ceunant Ash is unfossiliferous at this locality but is in turn overlain by highly fossiliferous, tuffaceous mudstones containing a diverse brachiopod-dominated fauna. Various elements of these lowermost Gelli-grîn faunas, in particular *Eoplectodonta*, are found so closely packed that in a few instances they show primary growth distortions; such a phenomenon indicates an *in situ* association. These fossiliferous beds are characterized by the following rapidly changing succession of local associations; an association dominated by *Onniella*, *Eoplectodonta*, *Bicuspina* and *Reuschella* is succeeded firstly by a *Nicolella*-dominated fauna, then by a *Skenidioides*-dominated fauna. These horizons are in turn overlain by beds containing *Dalmanella*, *Leptestiina* and *Howellites*. A species of the latter, *H. antiquior* (M'Coy), occurs in particular abundance in the middle part of the Gelli-grîn Formation and is associated with *Rhactorthis* and an abundance of the trilobites *Kloucekia*, *Broeggerolithus* and, to a lesser extent, *Flexicalymene*.

Although the middle part of the formation is not entirely exposed, examination of other contemporary sections has revealed that the *Howellites*-dominated fauna persists into sub-Cymerig beds. The change in facies associated with the onset of Cymerig Limestone deposition

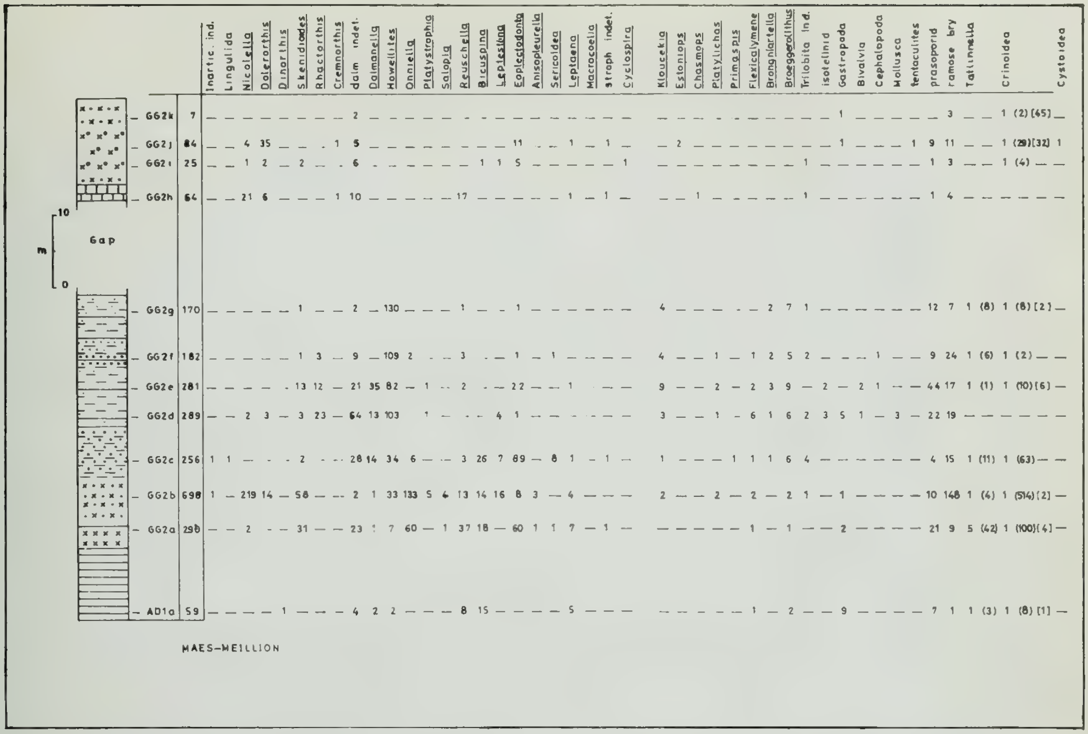


Fig. 13 Fauna from the Maes-Meillion section.

is accompanied by a corresponding change in the fauna. Cymerig and supra-Cymerig beds contain a fauna dominated by *Dolerorthis*, *Nicolella*, *Eoplectodonta* and *Skenidioides*. Other characteristic elements include *Cremnorthis*, *Chasmops* and *Estoniops*; the latter form is only known from horizons above the limestone member.

At Maes Meillion the faunal succession is remarkably similar to that recorded at Gelli-grîn (Figs 12, 13). Notable differences include the composition of the uppermost Allt Ddu fauna (dominated by *Bicuspina*, *Reuschella* and gastropods) and the occurrence of a fauna in the upper part of the Pont-y-Ceunant Ash Member which is thinner and finer here than to the north. The faunal succession throughout the formation mirrors the pattern observed in the Gelli-grîn section; all the dominant genera named above are found at equivalent horizons in this section 4 km to the south.

Three samples from newly-discovered Gelli-grîn exposures on Lledwyn Bach have yielded a fauna characteristic of the lower to upper middle part of the formation (i.e. from 5–10 m to 40–45 m above the base). The lowest, poorly-exposed beds contain an association characterized by *Eoplectodonta*, *Dalmanella*, *Howellites* and *Leptestiina* and are succeeded, after a 35 m gap, by larger outcrops yielding (from two sampled horizons 1 m apart) a fauna dominated by *Howellites* and trilobites (Fig. 7B, p. 178).

Analysis of the Gelli-grîn sequences in the Tan y Bwlch and Rhiw March sections reveals patterns of faunal succession in the lower and middle part of the formation which compare closely with those noted in the sections to the north (Figs 14–16). However, the faunal succession in the upper part of the formation differs from that recorded to the north and corresponds to a distinctive lateral facies change occurring south of Pen y Cefn Coch. At Tan y Bwlch the Gelli-grîn Formation is only about 45 m in thickness and is mainly argillaceous throughout.

The lower part of the formation at Tan y Bwlch is dominated by *Onniella* and *Eoplectodonta*,

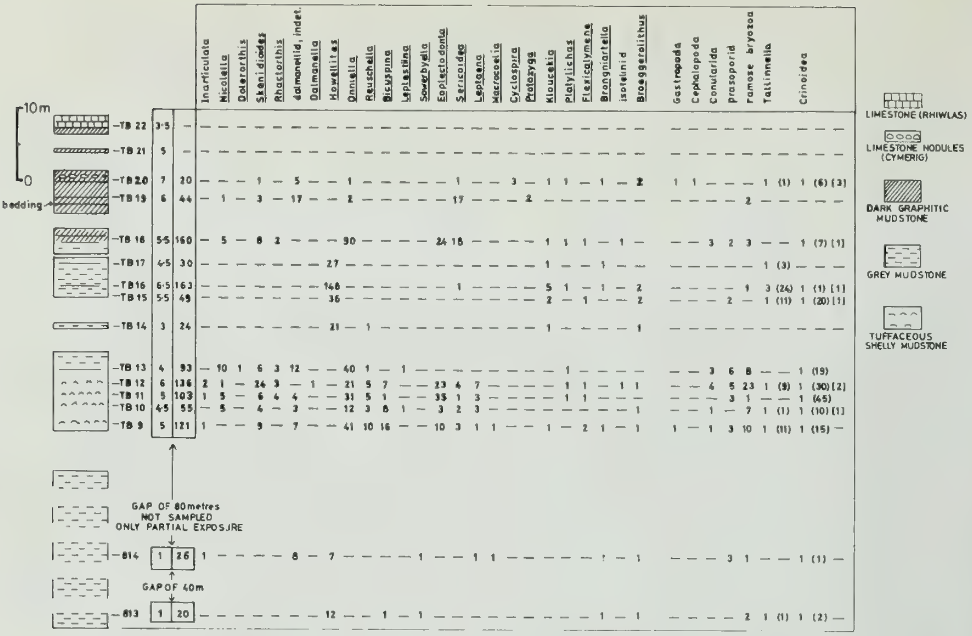


Fig. 14 Fauna from the Nant Tan y Bwlch section. (For Conularida read Macheridia.)

with *Skenidioides* and *Nicolella* also representing important elements. The middle part of the formation is dominated by *Howellites* and, to a lesser extent, *Kloucekia*, *Broeggerolithus* and the Ostracoda. However, in the uppermost part of the formation (i.e. the Dyfi Mudstone Member) the fauna is characterized mainly by *Sericoidea* and rarer forms like *Cyclospira*.

In the Rhiw March section the Gelli-grîn Formation has been sampled more thoroughly than at any other locality. The pattern of faunal distribution is similar to that noted in the Tan y Bwlch section. The lower beds are dominated by *Onniella* and *Bicuspina*, with *Eoplectodonta* being less abundant than at contemporary horizons to the north. The *Onniella*-dominated beds pass up into strata in which *Nicolella* and *Skenidioides* are important elements and are in turn succeeded by mudstones of the middle part of the formation which are dominated by *Howellites*, *Kloucekia*, *Broeggerolithus* and the Ostracoda. The upper (Dyfi Mudstone) part of the formation is dominated by *Sericoidea* and *Onniella* in association with less abundant forms including *Skenidioides*, *Cyclospira*, *Eoplectodonta*, *Nicolella*, various inarticulates and macheridians. The uppermost metre of the Rhiw March succession consist of soft, coal-black graptolitic shale containing a monospecific assemblage of *Climacograptus minimus* (Carruthers); specimens were not counted for inclusion in Fig. 15.

Non-dominant elements in the Gelli-grîn Formation. Throughout its area of outcrop the lowermost beds of the formation contain a number of brachiopod genera which are either unique to this part of the Lower Bala Group or only otherwise known from the Derfel Limestone. These genera include ? *Pseudolingula*, *Platystrophia*, *Anisopleurella*, *Oxoplecia*, *Palaeostrophomena* and *Bimuria*. Of these *Bimuria* was previously unknown in Wales and *Palaeostrophomena* and *Anisopleurella* were hitherto unknown in the Gelli-grîn Formation. *Salopia* is also characteristic of the lower part of the formation but, in addition to being known from the Derfel Limestone, is now also recorded from horizons beneath the Frondderw Ash in Afon Twrch. A few specimens assigned to *Kjaerina* (*Hedstroemina*) have been recovered from sample R28; this genus was previously only known from the Glyn Gower 'unit' of the Lower Bala Group (Williams 1963 : 460). The distribution of seven of the eight above-mentioned genera is shown in Figs 12–15; the eighth genus,

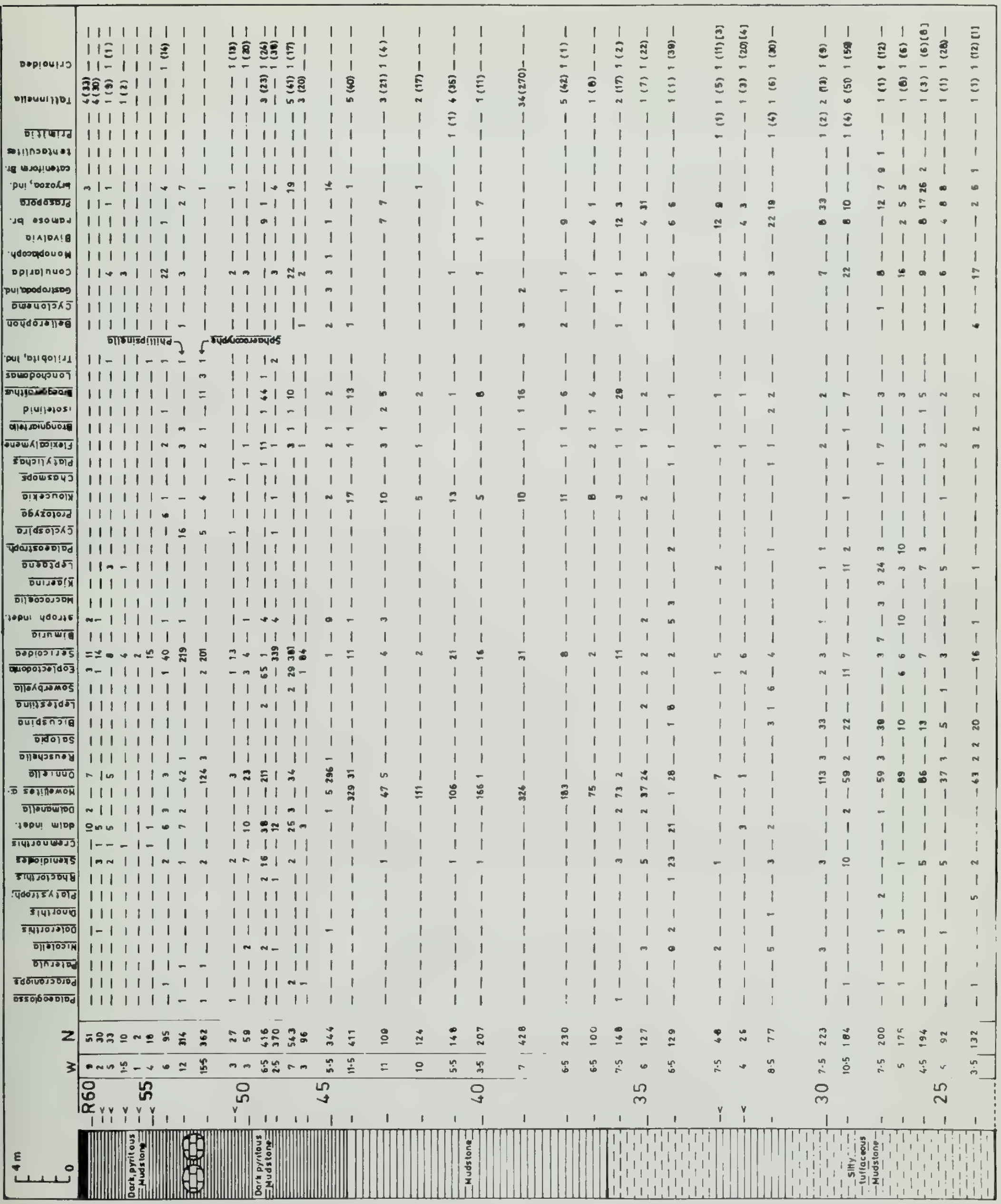


Fig. 15 Fauna from the Rhiw March section (Gelli-grîn/Nod Glas beds). (For *Bellerophon* read *Sinuites*, and for Conularida read Macheridia.)

Oxoplecia (not recorded in the samples from which the data tables were compiled) is now known to occur at horizons GG1c and GG1e (Fig. 12) and TB9 and TB12 (Fig. 13), following the examination of additional material.

The middle part of the formation generally contains fewer brachiopods and more trilobites than the lower beds. With the possible exception of *Rhactorthis*, less dominant elements show no significant restriction to the middle part of the formation. Conversely the distribution of *Paracraniops macellus* Williams suggests that this form has an affinity with the faunal associations of the lower and upper parts of the formation (Fig. 15).

The upper part of the formation has yielded several taxa which were hitherto unrecorded in the Upper Bala Group. These forms, which include *Paterula*, *Palaeoglossa*, *Protozyga*, *Phillipsinella*, *Lonchodomas* and *Sphaerocoryphe*, were all recovered from the Cymerig Limestone member or associated beds in the Tan y Bwlch and Rhiw March sections (Figs 14–15). The discovery of *Protozyga* at these localities represents the first record of this genus in Wales. The trilobites *Phillipsinella*, *Lonchodomas* and *Sphaerocoryphe* are all known from the Upper Bala Group of this area but were previously unknown at these earlier horizons. *Cyclospira* is an important element of the Cymerig fauna at these two localities; although recorded by Williams (1963) the material recovered in this study has facilitated a more thorough appraisal of the specific affinities and distribution of this form than was hitherto possible. Full taxonomic descriptions are given below, p. 219.

The Pistyll Gwyn, Y Ceunant and Aber-Cowarch sections

Fig. 17 contains faunal data derived from the study of the three above-named sections. These sections, the southernmost in the area under study, cover the uppermost 30 m of the Caradoc succession which, at all localities, comprises the Nod Glas Formation and a part of the underlying Ceiswyn Mudstone. The faunal succession is similar at each locality.

The grey mudstones underlying the Dyfi Mudstone are dominated by *Howellites* and, to a lesser extent, the trilobites *Kloucekia* and *Broeggerolithus*. These are succeeded by the rather more pyritous, grey Dyfi Mudstone which is dominated by the small brachiopod *Sericoidea*. The member is also characterized by the variable occurrence of *Kloucekia*, *Broeggerolithus*, *Cyclospira* and the Macheridia. At Pistyll Gwyn these mudstones contain a locally-developed phosphatic limestone which contains *Sericoidea*, *Broeggerolithus*, *Nuculites* and *Sinuites*. The discontinuous Cymerig Limestone Member, consisting of variably fossiliferous, crystalline nodules measuring about 30 cm × 15 cm, occurs at an horizon in the upper part of the Dyfi Mudstone.

Above the Cymerig Member the Dyfi Mudstone grades rapidly up into the sparsely fossiliferous or entirely unfossiliferous, dark grey Corris shale.

Faunal associations

Introduction

The data presented in Figs 4–17 represent as thorough a quantitative description of the faunal content of the succession as the sampling scheme allows. Since only a cursory glance at these data indicates that samples from like facies consistently contain recurrent combinations of taxa in similar proportions (whilst samples from other facies contain different combinations and proportions of mainly different taxa) it must be concluded that the associations are largely

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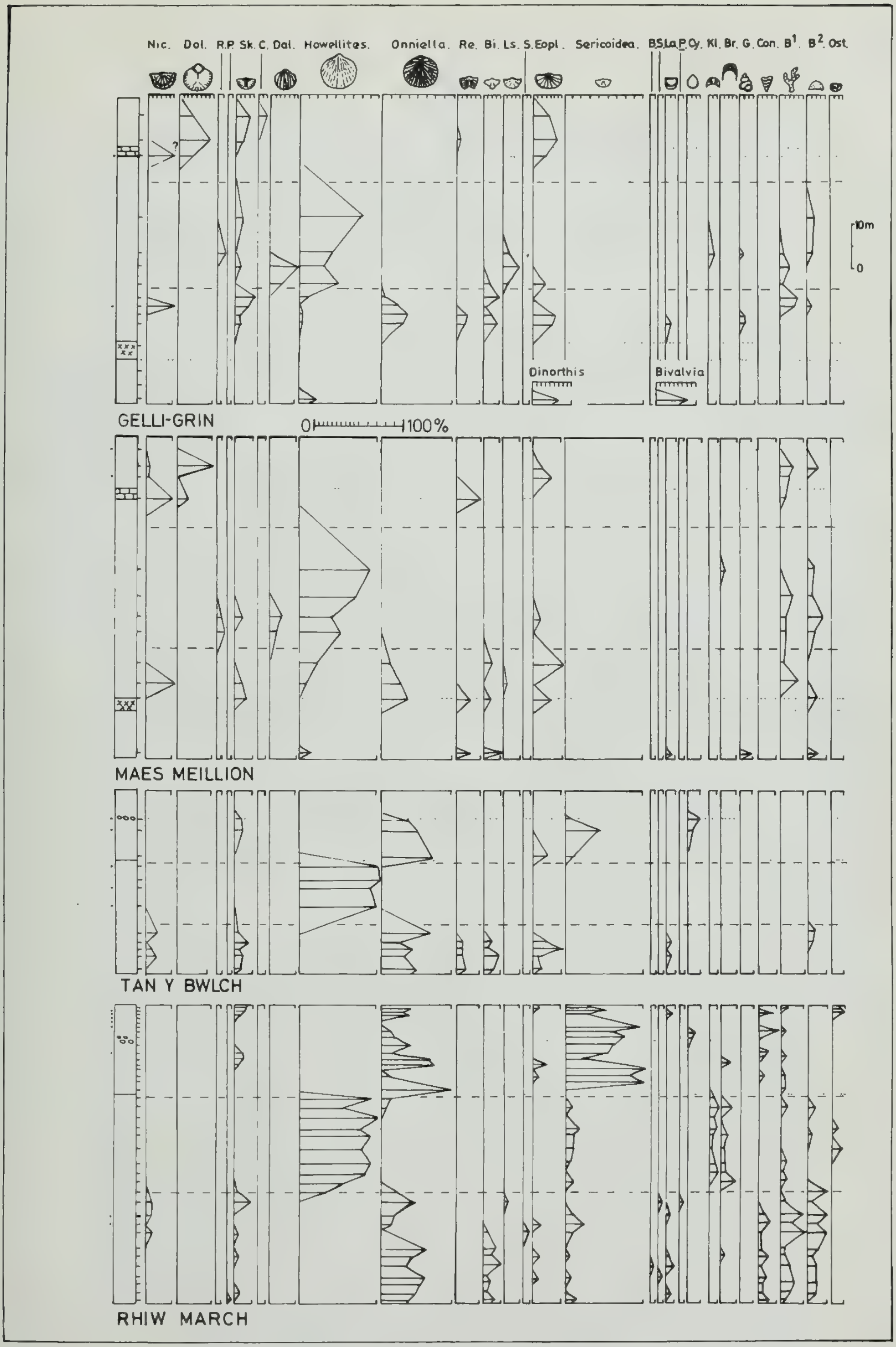
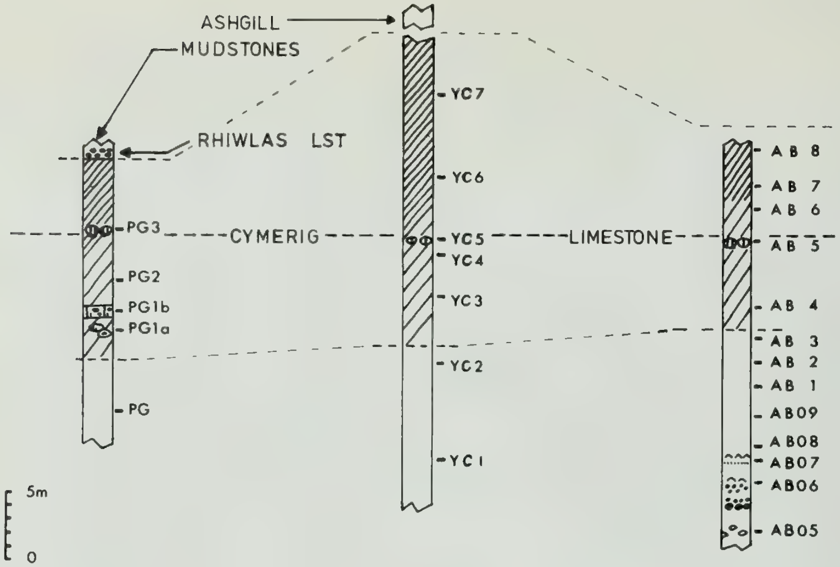
Fig. 16 Percentage distribution of taxa in named sections through the Gelli-grîn Formation. Abbreviations refer to *Nicolella* (Nic), *Dolerorthis* (Dol), *Rhactorthis* (R), *Platystrophia* (P), *Skenidioides* (Sk), *Cremnorthis* (C), *Dalmanella* (Dal), *Reuschella* (Re), *Bicuspina* (Bi), *Leptestiina* (Ls), *Sowerbyella* (S), *Eoplectodonta* (Eopl), *Bimuria* (B), Strophomenacea/*Macrocoelia* (S), *Leptaena* (La), *Palaeostrophomena* (P), *Cyclospira* (Cy), *Kloucekia* (Kl), *Broeggerolithus* (Br), Gastropoda (G), Macheridia (Con), ramose Bryozoa (B^1), prasoporid Bryozoa (B^2), Ostracoda (Ost). Dashed lines represent boundaries between faunal associations.


Nic.
Dol.
R.P.
Sk.
C.
Dal.
Howellites.
Onniella.
Re.
Bi.
Ls.
S.
Eopl.
Sericoidea.
B.
S.
La.
P.
Cy.
Kl.
Br.
G.
Con.
B¹.
B².
Ost.
?
10m
0
Dinorthis
Bivalvia
GELLI-GRIN
0 100%
MAES MEILLION
TAN Y BWLCH
RHIW MARCH


ASHGILL
MUDSTONES
RHIWLAS LST
PG3
CYMERIG
LIMESTONE
PG2
PG1b
PG1a
PG
YC7
YC6
YC5
YC4
YC3
YC2
YC1
AB 8
AB 7
AB 6
AB 5
AB 4
AB 3
AB 2
AB 1
AB09
AB08
AB07
AB06
AB05
5m
0

SAMPLE NO.	Inarticulata	Dalmanellidae, indet. (Howellites)	Reuschella	Sericoidea	Cyclospira	Kloucekia	Broeggerolithus	Trilobita, indet.	Ostracoda	Bivalvia	Bellerophon	Other Gastropoda	Conularida	Bryozoa	Crinoidea	Graptoloidea	Miscellanea?	TOTAL	DIVERSITY	SPECIMENS PER Kg
PG 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	(1)	(1)	-
PG 2	-	7	1	21	-	1(2)	1(1)	1	-	-	-	-	6	1	1(3)	-	-	40	8	-
PG1b	-	-	-	-	-	-	1(14)	1	-	(1)	-	1	-	-	-	-	1	7	(5)	-
PG1a	-	-	-	260	-	-	2(7)	-	-	-	1	-	1	-	-	-	-	264	4	-
PG	-	79	-	3	-	5(20)	5(20)	1	1(3)	-	-	-	-	1	-	-	-	95	7	-
YC 7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0
YC 6	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0.7
YC 5	-	1	-	12	-	-	1(3)	-	-	-	-	1	-	-	-	-	-	15	4	20
YC 4	-	-	-	53	-	-	-	-	-	-	-	-	1	-	-	-	-	54	2	36
YC 3	-	-	-	50	-	-	-	1	-	-	-	-	2	-	-	-	-	53	3	70.6
YC 2	-	47	-	31	-	1(3)	1(3)	-	-	-	-	-	-	-	-	2	-	82	5	82
YC 1	-	48	-	3	-	-	-	1	-	-	-	-	-	-	-	-	-	53	3	104
AB 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0
AB 7	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
AB 6	1	-	-	1	-	-	-	-	1(2)	-	-	-	-	-	-	6	-	3	3	0.6
AB 5	1	-	-	28	4	-	-	-	-	-	-	-	-	-	-	-	-	40	5	5
AB 4	-	1	-	55	1	-	-	-	-	-	-	-	-	-	-	-	-	57	3	32.6
AB 3	-	1	1	4	1	-(5)	1(4)	-	-	-	-	-	-	-	-	-	-	9	6	2.25
AB 2	-	63	-	-	-	1(1)	-	-	-	-	-	-	-	-	-	-	-	64	2	18.3
AB 1	-	112	-	3	-	-	-	-	1(1)	-	-	-	-	-	-	-	-	116	3	33.1
AB09	-	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	1	10.7
AB08	-	42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	42	1	7.0
AB07	-	112	-	7	-	-	1(1)	-	-	-	-	-	-	-	-	-	-	120	2	20
AB06	-	86	-	3	-	-	1(1)	-	-	-	-	-	-	-	-	-	-	90	3	90
AB05	-	4	-	9	-	-	-	-	-	-	-	-	1	5	-	-	-	20	5	6.2

Fig. 17 Fauna from the Pistyll Gwyn section (PG), the Y Ceunant section (YC) and the Aber Cowarch section (AB). (For *Bellerophon* read *Sinuites*, and for Conularida read Macheridia.)

facies-related and that the sampling procedures consistently provide an adequate census method. This being the case it is necessary to proceed by outlining distinctive associations and assemblages and testing that at least in the general sense they differ significantly from each other in terms of their overall composition.

Although the associations named here (see also Lockley 1978) were picked out initially by 'simple inspection' of the data (cf. Watkins 1975 : 48) samples considered representative of given associations were compared with each other and with those from other associations using the Similarity Index or Index of Affinity (Murray & Wright 1974 : 3; Rogers 1976 : 504–506). Details are given below. Furthermore, all numerical data are presented here (Figs 4–17) in such a way as to be readily available for subjection to further quantitative analysis.

The associations and assemblages defined here (in descending order of their stratigraphical occurrence) are as follows.

5. The *Onniella–Sericoidea* and the *Sericoidea* Associations from the Nod Glas Formation respectively north and south of Llanymawddwy
4. The *Howellites–Kloucekia* Association from the middle part of the Gelli-grîn Formation
3. The *Nicolella–Onniella* Association from the Lower part of the Gelli-grîn Formation (with variant earlier and later phases from the Derfel Limestone and upper part of the Gelli-grîn Formation respectively)
2. The *Howellites–Paracraniops* Association from the upper part of the Allt Ddu Formation
1. The *Heterorthis* Assemblage from respective upper and lower parts of the Llaethnant and Allt Ddu Formations.

The term 'assemblage' is used to distinguish clearly transported faunas from those considered to be either *in situ* or of the 'disturbed neighbourhood' type (*sensu* Scott 1974: 321), which are referred to here as 'associations'. The term 'phase' is used informally to indicate the different time intervals represented by the repetitive stratigraphical occurrence of the same (albeit varying) faunal association.

Although multivariate analysis has not been used to cluster like samples and to define associations, the use of the Similarity Index or Index of Affinity (IA) to test affinities between the majority of the larger representative samples (90 in all) serves the same purpose and clearly indicates that the associations named herein are relatively homogeneous in internal composition whilst being quite distinct from each other. Over 220 representative IA values consistently indicate that intra-association IA values are high whilst inter-association IA values are very low. For example, respective mean IA values for the *Howellites–Paracraniops* and the *Howellites–Kloucekia* Associations (with range in brackets) and number of IA values considered [in square brackets] are 61·4% (40–91%) [16] and 72·8% (37–98%) [54]. Similarly, respective values for the *Nicolella–Onniella* Association in the lower part of the Gelli-grîn Formation and the *Onniella–Sericoidea* Association are 57·4% (17–87%) [59] and 48·8% (7–83%) [36], whilst the phase of the *Nicolella–Onniella* Association in the upper part of the formation exhibits lower values, i.e. 40·8% (20–63%) [10]. Although mean IA values are below the 80% level considered to indicate 'identical assemblages' (Murray & Wright 1974 : 3), individual IA values above 80% are recorded for each of the associations except the phase of the latter one mentioned here which in any case is described from only a small number of samples. Mean IA values show a marked contrast to the low inter-association values calculated in order to compare the *Howellites–Kloucekia* Association with both the *Howellites-Paracraniops* Association and the *Nicolella–Onniella* Association (lower Gelli-grîn phase). Respective mean IA values (with range) and number of IA values used, as before, are 7·8% (3·2–13·2%) [4] and 9·9% (2·5–13·1%) [4]. An outline of these recognizable associations is presented in quantitative terms using the parameters of persistence of occurrence and mean relative abundance. Fig. 18 outlines the stratigraphical distribution of associations identified in the fossiliferous upper part of the Caradoc succession between Bala and Dinas Mawddwy, and Fig. 19 outlines their composition.

Calculations of the relative abundance of taxa from each sample (Figs 5, p. 177, 11, p. 182, 16, p. 189) permitted the construction of a series of tables (one for each sample) in which faunal elements were ranked in order of abundance (Lockley 1977). The numerically dominant taxa which make up 80% of the fauna may be regarded as the Trophic Nucleus; Neyman (1967) proposed this quantitative definition of the nucleus originally defined by Turpaeva (1948). The dominant faunas listed in Fig. 19 therefore represent the Trophic Nucleus of their respective named associations either at named localities or for the association as a whole.

Although some palaeontologists (e.g. Titus & Cameron 1976) have named associations or communities after their rarer component species, such methods do not conform with the more popular tendency of naming associations after their dominant component taxa. The classic work of Petersen (1924), summarizing his studies of marine animal communities in Danish waters, included an outline of four categories of component taxa – 1st, 2nd and 3rd order characterizing species and associated animals. Thorson (1957 : 477) subsequently proposed that these respective characterizing species be quantitatively defined as representing at least 5, 5, 10 and 2% of the total living weight (biomass) in at least 50, 50, 70 and 25% of samples from any given community.

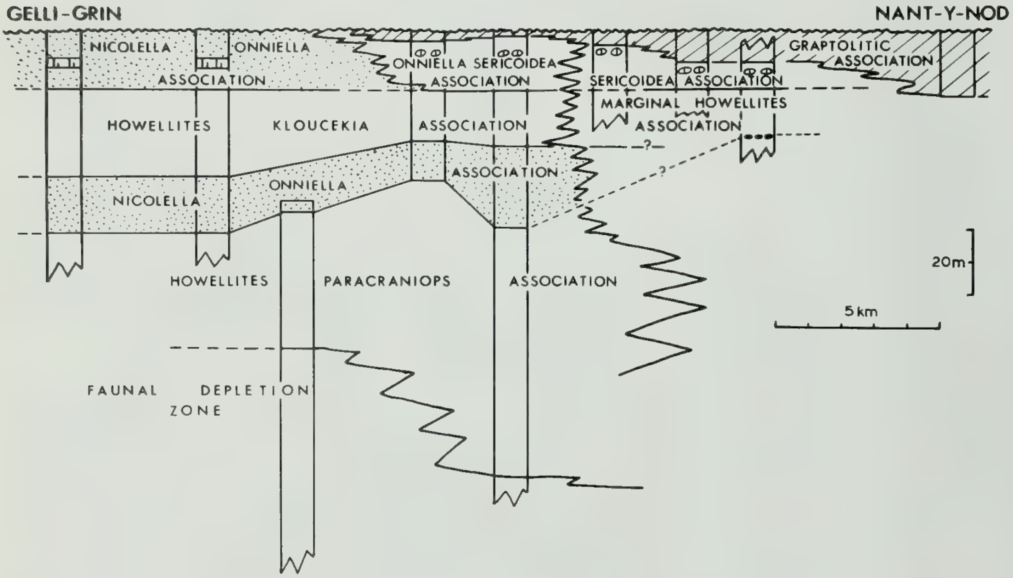

GELLI-GRIN
NANT-Y-NOD
NICOLELLA
ONNIELLA
ASSOCIATION
ONNIELLA SERICOIDEA
ASSOCIATION
SERICOIDEA ASSOCIATION
GRAPTOLITIC
ASSOCIATION
MARGINAL HOWELLITES
ASSOCIATION
HOWELLITES
KLOUCEKIA
ASSOCIATION
?
ONNIELLA
ASSOCIATION
NICOLELLA
HOWELLITES
PARACRANIOPS
ASSOCIATION
20m
5km
FAUNAL DEPLETION
ZONE

Fig. 18 Stratigraphical distribution of named faunal associations in the upper part of the Lower Bala Group (drawn to scale).

The only differentiation made between 1st and 2nd order characterizing species was that 1st order species occur 'practically everywhere' in a specific community whereas 2nd order species occur 'only in certain parts' of such specific communities. Biomass estimates cannot be derived from fossil associations without at least making numerous assumptions and repetitive measurements for the calculation of the mean size of each population. Nevertheless, in the absence of other evidence, relative abundance can be used as it is in this study as an alternative estimate of an association's composition. If this is done with the aim of identifying characterizing species it becomes clear that only the dominant species fall within this category.

Named Associations from the Caradoc Series of the Bala to Dinas Mawddwy area

Associations in the Allt Ddu Formation

(i) The *Howellites–Paracraniops* Association, characteristic of the upper part of the Allt Ddu Formation, contains no genera, other than these two and *Broeggerolithus*, which are representative of biospecies which could be considered strictly analogous to 1st or 2nd order characterizing species (Fig. 19). Although several other genera listed here occur in at least 50% of samples, in

TAXA/GENERA	OCCURRENCE	(%)	MEAN ABUNDANCE		OCCURRENCE	(%)	MEAN ABUNDANCE
A				**B**			
Howellites	12/12	100 %	53.45%		23/24	95.8%	37.42%
Paracraniops	12/12	100 %	11.95%		17/24	70.8%	7.13%
Bryozoa	12/12	100 %	5.98%		22/24	91.7%	13.35%
Broeggerolithus	12/12	100 %	4.02%		24/24	100 %	8.67%
Macrocoelia	10/12	83.3%	4.32%		8/24	33.3%	1.51%
Brongniartella	8/12	66.7%	1.19%		20/24	83.3%	2.03%
Ostracoda	5/12	41.7%	1.25%		19/24	79.2%	4.42%
Bivalvia	5/12	41.7%	1.13%		8/24	33.3%	0.75%
Gastropoda	5/12	41.7%	0.84%		16/24	66.7%	3.39%
Reuschella	4/12	33.3%	4.47%		5/24	20.8%	1.42%
Dinorthis	3/12	25.0%	1.20%		0/24	-	-
Leptaena	3/12	25.0%	0.80%		10/24	41.7%	1.73%
Sowerbyella	2/12	16.7%	3.78%		1/24	4.7%	0.84%
Bicuspina	2/12	16.7%	0.34%		14/24	58.3%	4.49%
Sericoidea	0/12	-	-		12/24	50.0%	3.48%
		TOTAL	94.72%			TOTAL	90.63%
C				**D**			
Onniella	26/26	100 %	27.52%		0/7	-	-
Bryozoa	26/26	100 %	17.11%		6/7	85.7%	14.18%
Skenidioides	23/26	88.5%	6.08%		4/7	57.1%	5.58%
Bicuspina	22/26	84.6%	7.11%		1/7	14.3%	0.57%
Eoplectodonta	18/26	69.2%	10.59%		5/7	71.4%	13.69%
Reuschella	17/26	65.4%	2.93%		3/7	42.8%	4.24%
Nicolella	15/26	57.7%	4.26%		5/7	71.4%	15.25%
Dolerorthis	7/26	26.9%	0.32%		7/7	100 %	19.28%
		TOTAL	75.92%			TOTAL	72.79%
E				**F**			
Howellites	21/21	100 %	65.98%		10/10	100 %	83.66%
Kloucekia	21/21	100 %	3.69%		3/10	30 %	0.80%
Broeggerolithus	20/21	95.2%	3.83%		4/10	40 %	0.84%
Sericoidea	12/21	57.1%	2.46%		7/10	70 %	10.34%
Skenidioides	11/21	52.4%	0.97%		0/10	-	
		TOTAL	76.93%			TOTAL	95.64%
G				**H**			
Onniella	16/16	100 %	36.77%		-	-	-
Dalmanellidae	-	-	-		3/7	42.8%	3.70%
Sericoidea	14/16	87.5%	38.39%		7/7	100 %	84.2 %
Bryozoa	13/16	81.2%	2.68%		-	-	-
Skenidioides	11/16	68.7%	4.51%		-	-	-
Conularida	11/16	68.7%	5.52%		4/7	57.1%	3.01%
Cyclospira	7/16	43.7%	2.27%		2/7	28.6%	1.68%
Ostracoda	7/16	43.7%	2.18%		-	-	-
Kloucekia	7/16	43.7%	1.13%		2/7	28.6%	0.71%
Eoplectodonta	6/16	37.5%	2.99%		-	-	-
Broeggerolithus	5/16	31.2%	2.25%		3/7	42.8%	1.42%
Nicolella	5/16	31.2%	0.59%		-	-	-
Graptoloidea	0/16	-	-		1/7	14.3%	2.14%
		TOTAL	99.28%			TOTAL	96.88%

Fig. 19 A & B. Dominant and persistent taxa/genera in the *Howellites–Paracraniops* association in the upper part of Allt Ddu Formation at Craig y Gath (A) and Rhiw March (B); in the *Nicolella–Onniella* association from the (C) lower and (D) upper parts of the Gelli-grîn Formation; in the *Howellites–Kloucekia* association from the middle part of the Gelli-grîn Formation (E) and the marginal *Howellites* association from the uppermost Ceiswyn Mudstone Formation (F); in the *Onniella–Sericoidea* association (for Conularida read Macheridia) (G) and the *Sericoidea* association (H) of the Dyfi Mudstone.

most cases their mean relative abundance is less than 5%. With the probable loss of soft-bodied representatives of the fauna in the process of fossilization, all relative abundance figures would tend to be proportional overestimates. It is therefore probable that even fewer species can be confidently considered analogous to characterizing species (*sensu* Thorson 1957).

Although it is only possible confidently to use samples with at least 20 individuals for the purposes of calculating relative mean percentages of taxa comprising associations, the calculation of mean diversity is derived from the consideration of all samples in order to avoid an overestimate of diversity. The *Howellites–Paracraniops* Association has a mean diversity of 9·68 but can locally be found to yield samples with a diversity of up to 17. The association is named after *Howellites ultimus* Bancroft and *Paracraniops glaber* sp. nov. (p. 204) which both occur persistently and relatively abundantly; respective values for the two sections studied are 95·8–100% occurrence (with mean relative abundance of between 37·4 and 53·5%) for *H. ultima* and 70·8–100% occurrence (with a mean relative abundance of between 7·1 and 12%) for *P. glaber*. *Broeggerolithus* (cf. *B. soudleyensis* Bancroft) is of equal importance, occurring in all samples with a mean relative abundance of between 4 and 8·7%. Bryozoa are also an important element of the fauna with two morphospecies (a prasoporid and a ramose bryozoan) representing 6–13·4% of the fauna in almost all samples (92–100%); see Fig. 19, p. 193. Amongst the other more important 'associated species' are *Macrocoelia prolata* Williams and *Reuschella horderleyensis undulata* Williams from the Craig y Gath section and *Bicuspina spiriferoides* (M'Coy), *Sericoidea* sp. and *Brongniartella* cf. *minor* (Salter) from the Rhiw March section, all of which occur in at least 25% of samples with a mean relative abundance of between 2 and 4·7%. The Gastropoda (including *Sinuites* sp. and *Cyclonema* sp.) are an important element of the association at the latter locality.

Although there is variation in the composition of the association between the two localities of Craig y Gath and Rhiw March its extent is insufficient to suggest the existence of more than one association at these horizons.

Associations in the Gelli-grîn Formation

The Gelli-grîn Formation is characterized by three stratigraphically successive associations (Figs 16, 18), which are here described in sequence. These are the *Nicolella–Onniella* Association (phase 2) and the *Howellites–Kloucekia* Association respectively from the lower and middle parts of the formation between Gelli-grîn and Rhiw March, and also the *Nicollela–Onniella* Association (phase 3) of the upper part of the formation between Gelli-grîn and Pen y Cefn Coch. This latter association is related to the association from the lower part of the formation and to the *Onniella–Sericoidea* Association of the Dyfi Mudstone.

(ii) The *Nicolella–Onniella* Association (phase 2). From the lower part of the Gelli-grîn Formation this is a high diversity association (mean 17·5) named after *Nicolella actoniae obesa* Williams and *Onniella ostentata* Williams. The latter form is particularly abundant (Fig. 19) and is associated with large numbers of *Eoplectodonta rhombica* (M'Coy). This association is to some extent similar in composition to the Derfel Limestone association (phase 1 of the *Nicolella–Onniella* Association), which includes *Dolerorthis tenuicostata* Williams, *Nicolella humilis* Williams, *Onniella* aff. *avelinei* Bancroft and *Eoplectodonta lenis* Williams amongst the most common Brachiopoda. The Derfel Limestone association is also of a high diversity, yielding up to 28 species from a single large sample; such values compare with maximum values of 25 for samples from the lower part of the Gelli-grîn Formation. The association from the upper part of the Gelli-grîn Formation (phase 3; mean diversity 13·7 and maximum 19) is also referred to here as the *Nicolella-Onniella* Association although it is again different in composition from the association in the lower part of the formation (Fig. 19). *N. actoniae obesa* Williams and *E. rhombica* (M'Coy) are common at horizons in both the lower and upper parts of the formation; however, *Dolerorthis duftonensis prolixa* Williams, which is uncommon from the lower part of the formation, occurs abundantly in the uppermost parts. *O. ostentata* Williams is not recognized from the upper part of the formation; the Dalmanellidae are poorly represented and assigned to *Onniella* sp., *Dalmanella* sp. or in a few cases *Bancroftina* sp.; Figs 7A, 12 and 13 do not distinguish between these three genera.

The composition of the *Nicolella–Onniella* Association (phase 2) from the lower part of the Gelli-grîn Formation is calculated from the analysis of samples GG1b–GG1e, GG2a–GG2c, ADZ, ADY, TB9–TB13 and R24–R35. The summary of these data, shown in Fig. 19, indicates that, at this level, *Onniella* and *Eoplectodonta* are analogous to 'characterizing species' with *Reuschella* and *Nicolella* representing 'associated' forms. Although *Skenidioides*, *Bicuspina* and *Reuschella* are important constituents of this association, conspecific forms also constitute a significant element in other associations; they cannot therefore be considered strictly analogous to 1st or 2nd order characterizing species in the *Nicolella–Onniella* Association.

There is some lateral variation in the composition of the lower Gelli-grîn faunal association; this corresponds to a decrease in sediment coarseness towards the SSW. The most notable changes are a relative increase in the abundance of *Bicuspina* and *Leptaena* in this direction and a corresponding decline in the abundance of *Eoplectodonta* and *Nicolella* (Figs 12, 13). Rare occurrence of *Sowerbyella* in the Rhiw March section are unique to the formation and indicative of the modification of this association towards the SSW.

(iii) The *Howellites–Kloucekia* Association. The middle part of the Gelli-grîn Formation is mainly argillaceous; representative samples from beds GG1f–GG1g1, GG2d–GG2g, TB14–TB17 and R36–R44 reveal a faunal association dominated by *Howellites antiquior* (M'Coy), *Kloucekia apiculata* (M'Coy) and *Broeggerolithus nicholsoni* (Reed). The association has a mean diversity of 12·7. Maximum diversity values in excess of 20 have been recorded from samples GG1g1, GG2d and GG2e; however, these are atypical in being recovered from horizons closely associated with overlying and underlying strata containing higher diversity associations. The other 18 samples, particularly those from Tan y Bwlch and Rhiw March, exhibit lower diversities; minimum values do not exceed 4.

Although *Kloucekia* and *Broeggerolithus* are considered to each represent less than 4% of the total fauna (Fig. 19) in this association (when using the arbitrary correction factor of 4 as a compensation for ecdysis), it is clear that a correction factor of say 2 or 3 would indicate a mean relative abundance analogous with that of 'characterizing' species. *Sericoidea*, whilst being analogous to an 'associated' species, is known to be mainly restricted to the two southern sections (Figs 12, 13). The occurrence of *Skenidioides* in most samples from the Gelli-grîn associations is noted.

(iv) The *Nicolella–Onniella* Association (phase 3). The composition of this in the upper part of the Gelli-grîn Formation differs from that noted for the related phases of the association elsewhere in the succession; for example, it is only at this level that *Dolerorthis duftonensis prolixa* Williams can be considered analogous to a characterizing species (Fig. 19). Differences in composition are thought to be directly related to the distinctive calcareous facies associated with the Cymerig Limestone Member north of Pen y Cefn Coch. Caradoc strata above the Cymerig member in this region consist predominantly of coarse, shelly calcarenites containing tuffaceous material and ? ferruginous oolites. At certain horizons (GG2k and sample 615) vertical crinoid stems and bryozoan fronds are noted; these are considered indicative of the rapid deposition of coarse material in a shallow-water environment. Bulk samples are only readily obtained from a few horizons in the Cymerig and higher beds; in general the limestones and associated rocks are unyielding enough to present practical sampling problems. Of the 9 samples collected in this study only 7 yielded sufficient specimens to permit the estimation of relative abundances (Fig. 19). Owing to the small number of relatively variably composed samples, it is considered that the only clearly-defined characteristics which distinguish this facies fauna from related associations elsewhere in the area is the relative dominance of *Dolerorthis* and *Nicolella* and the small numbers of dalmanellids.

(v) The *Onniella–Sericoidea* Association. This facies fauna is found in association with the argillaceous Dyfi Mudstone Member between Tan-y-Bwlch and Rhiw March (Fig. 18). It is laterally equivalent to the coarse, calcareous beds containing the continuous Cymerig Member north of Pen y Cefn Coch and, although containing the discontinuous 'distal' parts of the Cymerig Member south of this locality, otherwise represents the most marked lateral facies and faunal change observed in this study.

The association is dominated by *Sericoidea abdita complicata* subsp. nov. (p. 212) and *Onniella* sp., which between them represent over 75% of the total fauna and are the only forms analogous to 'characterizing 'species. Poor preservation (associated with relatively intense cleavage in this argillaceous facies) militates against sound statistical assessment of the *Onniella* specimens for a specific determination. Less distorted specimens from the Cymerig Member display only external features.

Cyclospira, *Skenidioides* and *Eoplectodonta*, together with the ostracod *Tallinnella*, can all be considered analogous to 'associated animals'. The association has a mean diversity of 10·9 with maximum values (up to 17) representative of the Limestone Member and associated more calcareous shales. *Broeggerolithus* and *Flexicalymene* are particularly abundant at certain horizons (e.g. R49) in the Rhiw March section.

Similarities between the fauna from this association and the *Nicolella–Onniella* Association to the north help substantiate correlations between quite different facies, respectively of argillaceous and coarse calcareous sediment (Fig. 18). It is of interest to note that *Nicolella*, *Dolerorthis*, *Eoplectodonta*, *Leptestiina*, *Reuschella*, *Rhactorthis*, *Leptaena*, *Flexicalymene*, *Cyclospira*, *Onniella* and *Sericoidea* are amongst the genera common to both associations; the latter three dominate in the *Onniella–Sericoidea* Association whilst the other forms, common to the north, are rarer here to the south. *Protozyga*, *Paterula*, *Phillipsinella*, *Lonchodomas* and *Sphaerocoryphe* are all unique to this association being currently unknown elsewhere in the area.

(vi) The *Sericoidea* Association, although related to the *Onniella–Sericoidea* Association, is considerably less diverse (mean diversity 4·25, maximum 8). The association characterizes the Dyfi Mudstone Member between Pistyll Gwyn and Aber Cowarch (Fig. 18). Representative samples (PG1a, PG1b, PG2, YC3, YC4, YC5, AB4 and AB5) indicate an association entirely dominated by *Sericoidea* with a few poorly-preserved macheridians and dalmanellids showing distribution patterns analogous to those of 'associated animals'. *Broeggerolithus*, *Kloucekia* and unidentifiable graptolites also occur. *Cyclospira* and a spired gastropod are known from the Cymerig member whilst additional molluscan material is known from the locally-developed underlying limestone beds at Pistyll Gwyn.

(vii) The Marginal *Howellites* Association. Samples PG, YC1–2, AB05–09 and AB1–2 (Fig. 17, p. 190) have yielded a low diversity (mean 3·25) *Howellites*-dominated fauna. Although preservation of most of the material is poor it has been possible to identify *H. antiquior* (M'Coy) as the dominant species (83·7%). *Sericoidea* is also 'characteristic' of this association; however, its abundance is almost one order of magnitude less than in the succeeding *Sericoidea* Association. *Kloucekia* and *Broeggerolithus* both occur relatively abundantly in beds underlying those associated with the first major influx of *Sericoidea* (i.e. samples PG, YC2 and AB3; Fig. 17). Elsewhere throughout these successions their distribution is variable.

The Marginal *Howellites* Association is clearly related to the *Howellites–Kloucekia* Association typical of the middle part of the Gelli-grîn Formation both in terms of faunal composition and stratigraphical relationships. However, since the Cowarch Phosphate Bed and associated shell beds may be contemporaneous with the Pont y Ceunant Ash (Lockley 1980), the Marginal *Howellites* Association could also have been established in the Abercowarch area in Lower Gelli-grîn times and subsequently migrated diachronously northwards in middle Gelli-grîn times.

(viii) The Graptolitic Association. The uppermost part of the succession in the Tan y Bwlch to Aber Cowarch sections (Figs 13–17) consists of dark grey or black graptolitic or virtually unfossiliferous shales referred to as the Corris Shale Member (Lockley 1977, 1980). These beds are lithostratigraphically equivalent to the graptolitic Nod Glas seen at the type locality Nant y Nod. Since these dark pyritous shales have yielded only one or two small shelly fossils (samples

YC6, AB6 and AB7), from lower beds, it is convenient to refer to the fauna of this member as a graptolitic association.

(ix) The *Heterorthis* Assemblage. The shell beds dominated by *Heterorthis* and *Sowerbyella* beneath the Frondderw Ash in the Llaethnant Siltstone in Afon Twrch are considered separately from the younger named associations described above. The distinctive shell beds are concentrated in only about 15 m of strata (samples H1–H19 and equivalents, see Figs 3–5, pp. 174–177), and are considered to represent transported assemblages. These richly fossiliferous beds are underlain and overlain by mudstones and siltstones which are generally sparsely fossiliferous (Fig. 3); mean percentage values from these small samples would be of little value. Even within the shell bed sequence there are sudden changes in the composition of the faunas at successive horizons; samples H2, H4–H6 and H16–H19 are dominated by *Sowerbyella*, sample H7 is dominated by *Reuschella* and the Dalmanellidae whilst samples H8–H15 are dominated by *Heterorthis*. Mean Index of Affinity (IA) values for samples H8–H15 and H16–H19 respectively are 84·3 and 88·2; these contrast markedly with the IA value of 5·0 derived from a comparison of samples H15 and H16 and serve to demonstrate just how pronounced the sudden changes in faunal composition are. Similarly, the mean diversity of taxa (species) in the shell bed sample H1–H19 is 11·25 (maximum value 17) whereas the mean diversity for overlying samples H20–H29 is 4·5 (maximum 9).

The composition of faunas above and below the shell beds is essentially similar to that observed in less fossiliferous parts of the Allt Ddu, Glyn Gower and Llaethnant Formations and so could be considered a poorly-developed expression of the *Howellites–Paracraniops* Association described from the upper part of the Allt Ddu Formation.

In contrast, however, the shell beds containing *Heterorthis* cf. *retrorsistria* (M'Coy) and *Sowerbyella sericea permixta* Williams, whilst being reminiscent of the *Heterorthis* 'faunule' (*sensu* Bassett *et al.* 1966 : 237), contain *Onniella ostentata* Williams, *Nicolella* sp., *Orthisocrania* sp., *Salopia* sp., *Dolerorthis* sp. and *Chasmops* sp., all of which are considered characteristic of the *Nicolella–Onniella* Association. They are also characterized by significant numbers of *Dinorthis* and *Reuschella* and various cephalopod and gastropod species.

Although the relationship between this *Heterorthis–Sowerbyella* Assemblage and its rare elements is unknown, it is reasonable to assume that a *Nicolella–Onniella* type of association was established locally in pre-Frondderw times.

Diversity patterns

There are various methods by which relative diversity values D may be calculated. The two methods chosen here are the Margalef method which uses the formula $D=(S-1)/\log N$ (Margalef 1958) and the Sanders (1968) rarefaction technique which is similarly designed to calculate diversity values for a standard sample size (in this case 50 individuals). Both methods have been applied to palaeoecological studies; for example, Ziegler *et al.* (1968) used the Margalef index in the modified form $D=S/(\log N)$, and various authors including Calef & Hancock (1974), Antia (1977), Fürsich (1977) and Watkins (1979) have used the Sanders rarefaction techniques.

MacArthur (1965 : 511) stated that the simplest measure of species diversity was a count of number of species. Similar simple definitions of species diversity or species richness given in numerous standard texts, e.g. Krebs (1978 : 374) and Valentine (1973 : 288), usually refer to community diversity but may equally well be applied to the diversity of individual samples.

Since a simple count of species diversity is a prerequisite for the calculation of relative diversity values in a series of samples, the original, size-dependent diversity values are plotted alongside standardized values for comparative purposes (Figs 20, 21).

The two standardizing methods applied here have the effect of smoothing out patterns of excessive fluctuation which are related to sample size; they also serve to emphasize real patterns of variation like the pronounced fluctuations observed in the Rhiw March succession (Fig. 20). Here a moderately diverse association in the lower part of the sampled Allt Ddu succession is succeeded by less fossiliferous strata, with a less diverse fauna, in the uppermost part of the

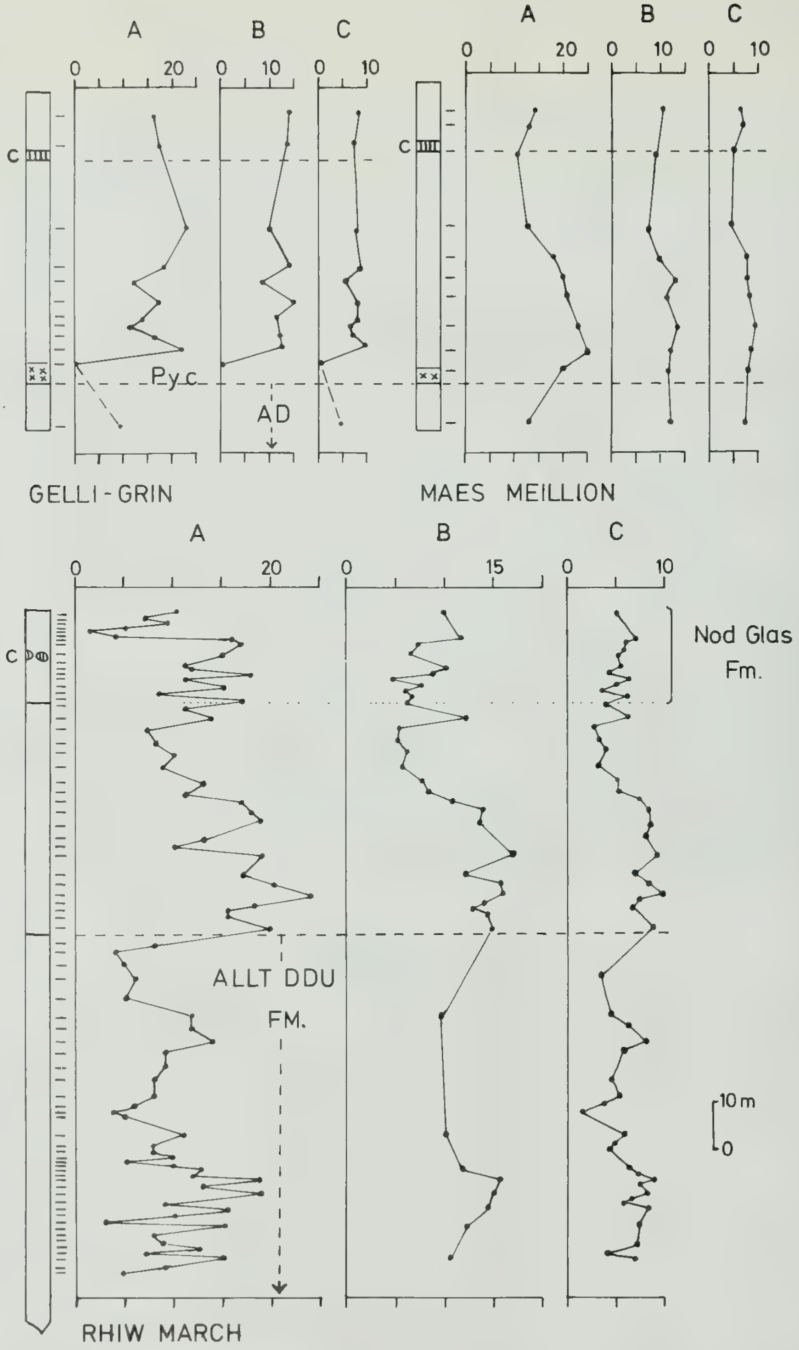


Fig. 20 Faunal diversity patterns in parts of the Allt Ddu (AD) and Gelli-grîn Formations (including the Cymerig (C) and Pont y ceunant (Pyc) Members) at three named localities. A represents species per sample; B represents diversity values standardized to a sample size of 50 individuals using the Sanders (1968, 1969) rarefaction technique; C represents diversity values derived from the Margalef (1958) index.

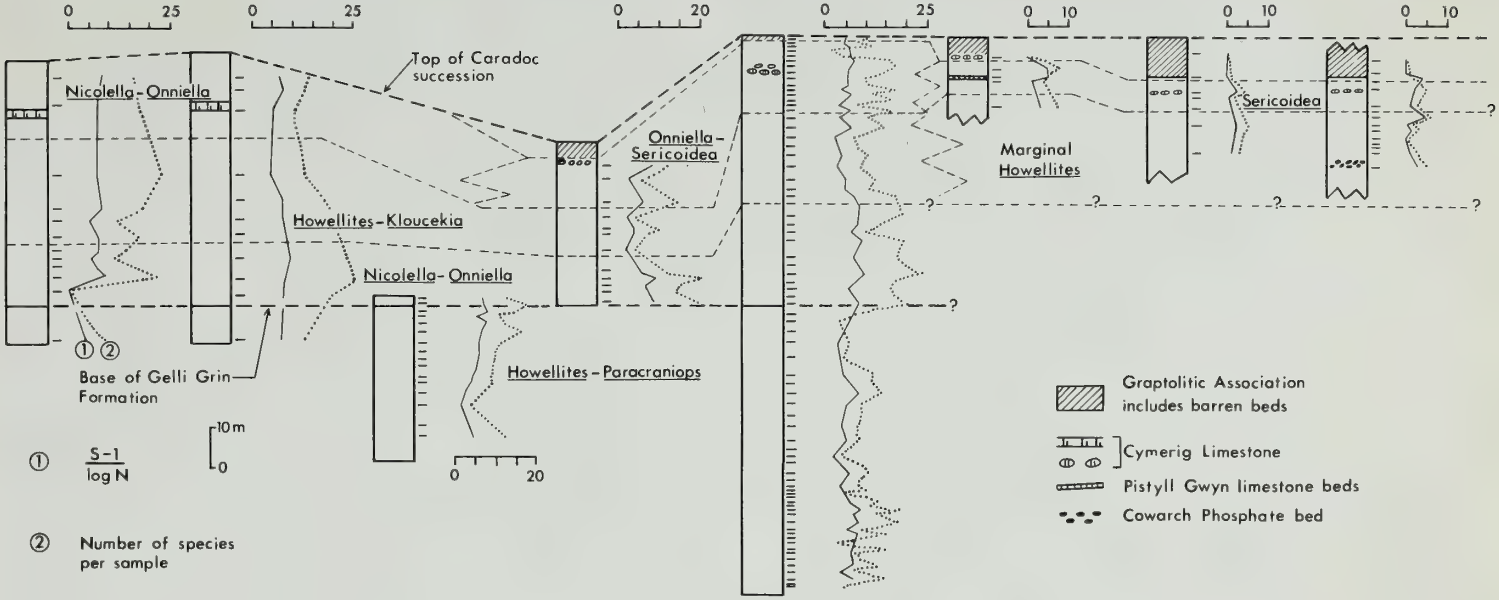


Fig. 21 Faunal diversity patterns and their relationship to faunal associations.

formation; these beds are in turn succeeded by those of the lower part of Gelli-grîn Formation which contain a high-diversity association related to a less argillaceous, calcareous facies. The middle part of the formation, representing a return to more argillaceous deposition, is characterized by a low-diversity association which contrasts with the associations of higher diversity of both the preceding and succeeding beds.

The use of the Sanders rarefaction technique generally involves adherence to a particular, chosen sample size. In this case, the use of diversity values calculated for a sample size of 50 avoids the necessity of calculating diversity values for smaller samples, although this may be done if desired. When used in isolation no such restraints affect the use of the Margalef diversity index which produces size-dependent results; however, size-related variation in diversity values is not excessive in this case where values for N vary only within a single order of magnitude. In the present study Margalef diversity values were calculated only for samples with at least 20 individuals, except in the southernmost three sections where a few samples associated with the Graptolitic Association are characterized by minimal numbers of specimens. The estimation of the Sanders and the Margalef indices has the primary effect of reducing the numerical value of the original whole-number count of species per sample to non-integral numbers of little more than 50% of the value of original counts; the latter method results in greater reductions (Fig. 20).

Although the diversity indices used here do not take into account species equitability (or evenness of distribution of species within samples or associations) it is to be expected that low-diversity associations would exhibit less even distributions than high-diversity associations (Pielou 1969 : 233; Krebs 1978 : 456). Such relationships are intuitively evident in the case of the associations discussed here. Although detailed discussions of species equitability are outside the present scope, following the above positive diversity/equitability correlation we may say, for example, that the *Sericoidea*-dominated association and the two dominated by *Howellites* have less equitable species distributions than the diverse *Nicolella–Onniella* Association.

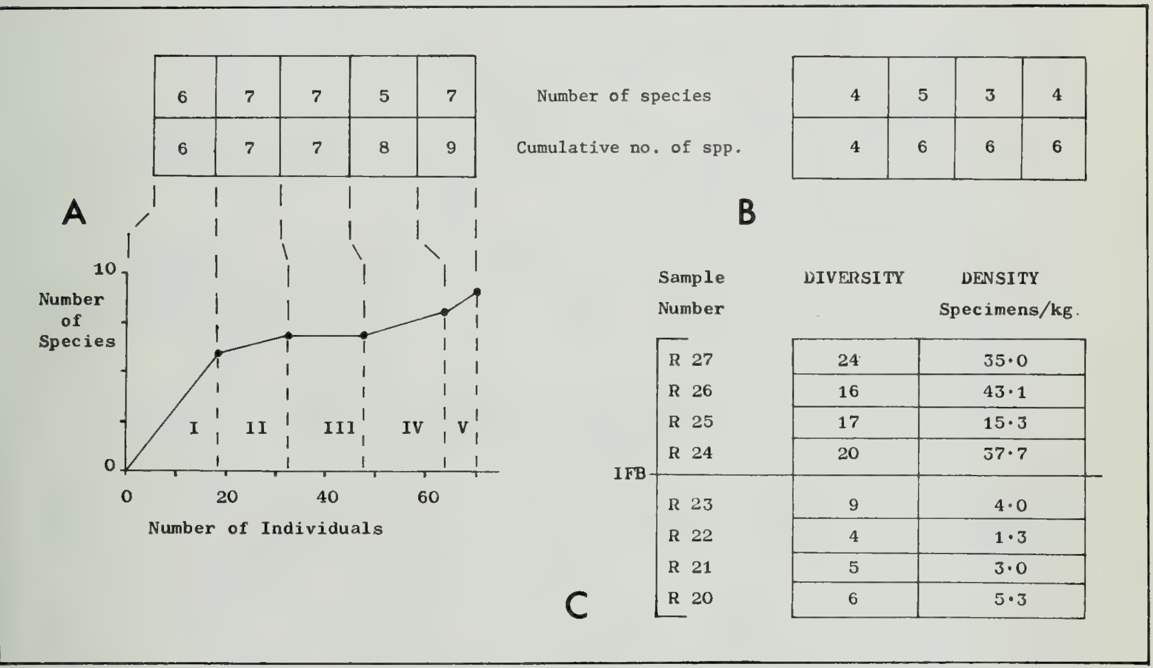
Since the Sanders method is limited to a particular sample size and produces values which fall between those calculated by the other two methods used here (Fig. 20), it was not used in the compilation of Fig. 21. Here, the two most different diversity indices are plotted for all the main thoroughly-sampled sections (other than the Afon Twrch shell bed section) and shown in conjunction with the stratigraphical distribution of named faunal associations. In addition to the parallel patterns resulting from the application of differing methods to the same data, the most striking features of the stratigraphical variation in diversity trends are as follows. Firstly, it is apparent that there is a continual fluctuation in the diversity of sequentially collected samples; this has been noted by Watkins (1979) and can be attributed to a number of possible factors including patchiness of faunal distribution within associations, actual original fluctuations of diversity with time and differences in *post-mortem* disturbance at successive horizons or variations, including variations in fossilization processes, in the physical environment. The second distinctive pattern pertains to the relationships between faunal associations and diversity trends; Fig. 21 serves as a comprehensive graphic description of inter- and intra-association diversity trends. The relatively high diversity values noted for the *Nicolella–Onniella* Association from the lower part of Gelli-grîn Formation contrast with lower values noted for both the underlying and overlying associations and indicate that the variation in trends is directly related to original differences in the composition of these associations. Therefore, although short-term fluctuations cannot be unequivocally explained, longer-term variations can be accounted for to some degree.

Relationships between density and diversity

In lower parts of the succession it was found difficult to derive a statistically-valid sample (e.g. 50 individuals) from sparsely fossiliferous rock. For this reason tests were devised to establish whether low diversity values were an actual phenomenon or the product of small numbers of individuals in a sample (i.e. low density). Since high- and low-density samples often show similar patterns of taxonomic composition significant increases in diversity would probably not result from corresponding increases in sample size.

Two large collections, H29 (10 kg) and H26 (8 kg), from the sparsely fossiliferous lower Allt-Ddu Mudstones of the Afon Twrch section were chosen for testing. Each sample was divided into

2 kg 'sub-samples' of rock and the total fauna from each was broken out and identified separately. A consistent number of taxa was derived from each of these sub-samples and the cumulative number of taxa was found to increase only gradually as the data from each sub-sample were pooled (Fig. 22). A χ^2 test revealed that there is no significant difference between the taxonomic diversity in a small (2 kg) sample and a larger (8–10 kg) one; for H29 $98\% > P > 95\%$ and for H26 $95\% > P > 90\%$. This implies a positive relationship between low density and low diversity.



Number of species	6	7	7	5	7
Cumulative no. of spp.	6	7	7	8	9

Number of species	4	5	3	4
Cumulative no. of spp.	4	6	6	6

Sample Number	DIVERSITY	DENSITY Specimens/kg.
R 27	24	35·0
R 26	16	43·1
R 25	17	15·3
R 24	20	37·7
IFB		
R 23	9	4·0
R 22	4	1·3
R 21	5	3·0
R 20	6	5·3

Fig. 22 A, χ^2 data for sample H29 with graph showing cumulative number of species and individuals derived from five 2 kg subsamples comprising a 10 kg sample. B, χ^2 data for sample H26, divided into four 2 kg subsamples. C, χ^2 data for test of density–diversity relationships in a part of the Rhiw March section. IFB: interformational boundary.

Further evidence of such a relationship results from the analysis of a series of samples from contrasting facies (Fig. 22). Eight samples collected through 16 m of strata and across a facies boundary all show a positive correlation between density and diversity (χ^2, $50\% > P > 20\%$). Conditions favourable for increased diversity therefore favour increased numbers of individuals; conversely, factors limiting diversity tend also to limit numbers.

Such positive density–diversity correlations as those noted here are by no means universally evident; many authors have sought to demonstrate an inverse relationship between the two parameters. For example, Calef & Hancock (1974 : 779) and Hancock *et al.* (1974 : 151) referred to a negative correlation between density and diversity in their respective analyses of Silurian benthic communities.

Valentine (1972 : 195) stated that there was no single, well-verified theory of diversity regulation. Many environmental factors, including temperature, temperature stability, depth, salinity, current activity and substrate composition affect the diversity and density of benthic associations. The present author, like many workers, avoids considering any single factor in isolation and tends to favour unifying theories such as the 'stability-time hypothesis' (Sanders 1969).

Taxonomic descriptions

The main aim of this section is to describe and figure genera and species hitherto unknown in the Lower Bala Group. Amongst these are representatives of the trilobite genera *Cyphoproetus*, *Lonchodomas*, *Phillipsinella* and *Sphaerocoryphe*. Species of the brachiopod genera *Bimuria* and *Protozyga* are recorded in Wales for the first time. Excluding *Cyphoproetus*, the above-mentioned genera are from the Gelli-grîn Formation (at Rhiw March) and current evidence suggests that their distribution elsewhere is very restricted. Representatives of the brachiopod families Obolidae and Paterulidae, together with species of the genera *Orthisocrania*, *Paracraniops*, *Palaeostrophomena*, *Anisopleurella*, *Sericoidea* and *Cyclospira*, are described and figured. Although species belonging to some of these taxa are already known from the Lower Bala Group, those described here are either new species, species new to the area or well-preserved specimens of previously poorly-represented species. New representatives of the Lingulacea recovered during the present study are given only a generic classification because they cannot be assigned with confidence to any more specific taxonomic grouping owing to their lack of internal morphological features. This precludes lengthy discussion of diagnostic features, so only brief descriptions accompany certain plates.

Dr P. J. Brenchley has recovered several specimens of the brachiopod genus *Parastrophinella* from the Caradoc Bryn Beds of the NE Berwyns. Since this genus was hitherto unknown in the Caradoc of north Wales, and has only been recorded in the Caradoc of Salop and south Wales (Williams 1974, Addison 1974), the Berwyn material is best described in conjunction with new material from the Lower Bala Group.

Representatives of the Mollusca (6 genera) and the Echinodermata (2 species) are also figured.

Measurements for most of the material are included; however, values in brackets refer to variably distorted specimens and should therefore be regarded only as approximate estimates of original size.

Further information on those brachiopod species (and related forms) not fully described here may be found in Williams (1963) and Hurst (1979); similarly for information on the Trilobita see Whittington (1962–68).

Phylum **BRACHIOPODA** Dumeril, 1806
Class **INARTICULATA** Huxley, 1869
Order **LINGULIDA** Waagen, 1885
Superfamily **LINGULACEA** Menke, 1828
Family **OBOLIDAE** King, 1846
Subfamily **LINGULELLINAE** Schuchert, 1893

Genus *LINGULELLA* Salter, 1866

? *Lingulella* sp.
Fig. 24

Description. Suboval, convex specimen of exfoliated *Lingulella*, with pedicle valve 80% as wide as long and an acute beak (< 90°); ornamented with concentrically-arranged growth lines numbering at least four per mm at 3 mm anterior of the umbo, with fine fila between growth lines.

Material and locality. Complementary internal and external parts (BB92200a, b) of exfoliated pedicle valve (length 8 mm, width 6·5 mm, depth at umbo 0·7 mm) from fossiliferous shales at Pont Aber Derfel (SH 850395), the type locality for the Derfel Limestone.

Discussion. This is the first record of a genus belonging to the Inarticulata in this oldest member of the Lower Bala Group.

Lingulella cf. ***ovata*** (M'Coy, 1846)

Fig. 25

Description. Suboval, convex specimen of a pedicle valve 70% as wide as long and with an acute beak (< 90°). Ornamented with fine concentric growth lines seen only at anterior commissure (spacing 0·3 mm).

Material and locality. Complementary internal and external parts (BB92201a, b) of exfoliated pedicle valve from bed R36 in the Gelli-grîn Formation at Rhiw March.

Genus ***PALAEOGLOSSA*** Cockerell, 1911 (emend. Williams 1974)

Palaeoglossa cf. ***attenuata*** (J. de C. Sowerby, 1839)

Figs 26, 27

Description. Subtriangular convex pedicle valve 65% as wide as long with an acute beak (60° ± 5°), ornamented with strong concentric growth lines (2 per mm) in addition to fine fila.

Material and locality. Measurements in mm.

	length	width	depth
External mould of conjoined valves (BB92202) from bed GG1d .	14	9	1·5
Internal and external part of an exfoliated pedicle valve (BB92203a, b) from bed R52	10	6.5	–

Discussion. *P.* cf. *attenuata* is recorded here in the Lower Bala Group for the first time.

Subfamily **GLOSSELLINAE** Cooper, 1956

Genus ***PSEUDOLINGULA*** Mickwitz, 1909 (emend. Williams 1974)

? ***Pseudolingula*** sp.

Fig. 28

Description. Parallel-sided, convex glossellinid 42% as wide as long with an acute beak (< 90°) and ornamented with (poorly preserved) growth lines.

Material and locality. An external mould of a brachial valve (BB92204), length 24 mm, width 10 mm, was recovered from bed GG1b in the Gelli-grîn Formation.

Discussion. *Pseudolingula* is recorded here in the Lower Bala Group for the first time.

Family **PATERULIDAE** Cooper, 1956

Genus ***PATERULA*** Barrande, 1879

Paterula sp.

Figs 29a, b, 30

Description. Smooth oval *Paterula* with rounded posterior and anterior margins. 76–84% as wide as long, beak poorly defined. Well-developed marginal limbus.

Material and locality. Single specimens of the external and internal moulds of convex pedicle (?) valves (BB92205, BB92206) respectively from beds R52 and R53 in the Cymerig Limestone at Rhiw March.

Discussion. *Paterula* is recorded here in the Lower Bala Group for the first time.

Family **CRANIOPSIDAE** Williams, 1963

Genus ***PARACRANIOPS*** Williams, 1963

Paracraniops cf. ***macellus*** Williams, 1963

Figs 32a, b

Description. Elongately oval and subequivalve *Paracraniops*, with flattened posterior margin and strong concentric ornamentation consisting of 7–8 irregularly-spaced growth lines per mm on the anterior part of valve.

Material and locality. Five well-preserved external moulds were obtained from beds GG2c (BB92208), R29 (BB92263), R46 (BB92264) and R47 (two specimens) in the Gelli-grîn Formation.

Discussion. Williams (1963 : 347–348) discussed the problems of differentiating between pedicle and brachial valves belonging to this genus and revised his earlier diagnosis (1962 : 88–89) of which valve was which, concluding that the pedicle valve bears the shield-shaped muscle scars while the brachial valve bears posterior adductor and oblique scars extending anterolaterally for about a quarter of the valve length. Mitchell (1977 : 22–23) apparently ignored Williams' later proposals, preferring to adhere to his earlier definitions. However, the more recently proposed orientation is adhered to here and it is noted that *P. glaber* sp. nov. has distinctive posterior adductor (?) scars (Figs 33–36).

When describing *P. macellus*[1] (Williams 1963 : 348; pl. 1), insufficient material was available to illustrate the external morphology adequately and the reader was referred to descriptions of *P. pararius* Williams (1962), emend. Williams (1963) for additional information. Material obtained during this study shows the close resemblance between the exterior morphology of *P.* cf. *macellus* and *P. pararius*.

Paracraniops glaber sp. nov.

Figs 33–36

Diagnosis. Large, externally smooth, oval, dorsibiconvex (?) *Paracraniops* with well-developed limbus, slightly convex to asymmetrically conical dorsal (?) valve and slightly convex ventral (?) valve.

Name. 'Smooth'.

Description. Oval *Paracraniops* 66–84% as wide as long in populations with smaller and larger mean size respectively. Dorsal (?) valve with pair of variably-developed faint posterior adductor scars (?) arising anterior to the posterior margin (10% of valve length) and extending for 20–30% of valve length, only known in large specimens (Figs 33, 34). External ornament smooth except for well-developed marginal limbus. (Rare development of concentric growth lines seen on some internal moulds.)

Type material. Measurements in mm.

	length	width
Holotype, internal mould of brachial (?) valve, BB92209	5·5	4·8
Paratype, internal mould of pedicle (?) valve, BB92210	5·0	4·2
Paratype, internal mould of brachial (?) valve, BB92211	(4·5)	(4·1)
Paratype, internal mould of brachial (?) valve, BB92212	3·4	3·0

Type horizon and localities. Fig. 23 gives biometric parameters of specimens of *P. glaber* sp. nov. from sample loc. 55 near Fedw Farm (9089 2975) and from the Rhiw March section (Fig. 9, p. 180). The former locality, on the south side of Nant Rhyd Wen (opposite the cliffs of Craig y Gath), is the 'alternative' type locality for the Allt Ddu Formation (p. 178). Fig. 45A, p. 208, gives statistics of two small populations of *P. glaber* from beds R093 and R096 in the Rhiw March section.

Discussion. The morphology of most of the specimens belonging to this common Allt Ddu species is so featureless that previous studies have disregarded them owing to uncertainty about their taxonomic affinity (Williams, personal communication 1976). However, a fortuitous discovery of a small population of well-preserved, large *Paracraniops* specimens in a partially decalcified calcareous nodule has revealed that a few of these normally featureless valves have internal muscle scars preserved. The internal morphology of the dorsal (?) valve closely resembles that of *P. pararius* Williams, but the lack of external ornament on *P. glaber* distinguishes it from other related forms at least at the specific level. *P. glaber* appeared much earlier in the Lower Bala Group than the related form *P. macellus* Williams, which is only known from the Gelli-grîn Formation.

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[1] Called by Williams *P. macella*; however, a ruling of the I.C.Z.N. (1974, *Bull. zool. Nom.*, London, **31** : 81–83) is that generic names in *-ops* shall be regarded as masculine in all cases.

The mean length/width ratio of *P. glaber* varies allometrically with growth. Specimens from loc. 55 apparently grew to a relatively large size, increasing in width relative to length.

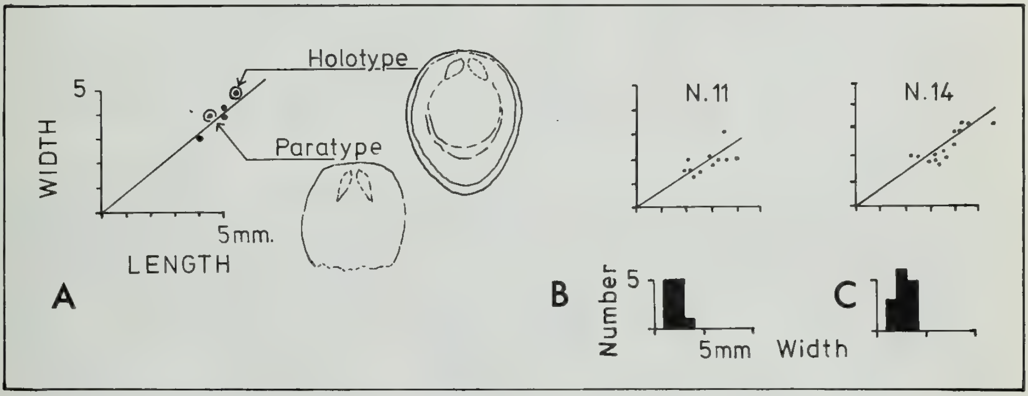


Fig. 23 Biometric parameters (length and width) of *Paracraniops glaber* sp. nov. A, specimens from sample 55 including two showing dorsal (?) muscle scars. B and C respectively represent specimens from samples R096 and R093; corresponding size frequency histograms are also shown.

Paracraniops cf. ***glaber*** Lockley, herein
Fig. 37

Material and locality. A single slightly distorted internal and external mould (BB92213a, b) of a specimen apparently conspecific with *P. glaber* recovered from bed H6 (9001 2305) is figured. The dorsal (?) posterior adductor scars and well-developed internal growth lines are seen. (Length of specimen 4·6 mm, width 3·1 mm.)

Suborder **CRANIIDINA** Waagen, 1885
Superfamily **CRANIACEA** Menke, 1828
Family **CRANIIDAE** Menke, 1828
Genus ***ORTHISOCRANIA*** Rowell, 1965
Orthisocrania sp.
Figs 31a, b

Description. Subcircular, convex brachial valve with elliptical anterior adductor scars.

Material and locality. Single internal mould of deformed brachial valve (BB92207) from bed H8 in Afon Twrch (9001 2305); see Fig. 4, p. 176.

Discussion. This is the first record of *Orthisocrania* from beds below the Gelli-grîn Formation. This Soudleyan occurrence, the earliest known in Britain, was predicted by Wright (1970 : 102).

Class **ARTICULATA** Huxley, 1869

Introduction. Systematic descriptions of members of this class are given for representatives of the Orders Strophomenida, Pentamerida and Spiriferida only. Although representatives of seven species in the Order Orthida are figured, they are all considered to be conspecific with those described by Williams (1963); they are included in order to illustrate well-preserved morphological features and, in the case of *Nicolella* cf. *actoniae obesa*, *Onniella ostentata* and *Salopia* sp., represent early occurrences of species previously known only from the Gelli-grîn Formation.

Order **ORTHIDA** Schuchert & Cooper, 1932
Superfamily **ORTHACEA** Woodward, 1852
Family **ORTHIDAE** Woodward, 1852
Subfamily **PRODUCTORTHINAE** Schuchert & Cooper, 1931

Genus ***NICOLELLA*** Reed, 1917

Nicolella cf. ***actoniae obesa*** Williams, 1963
Fig. 38

MATERIAL, LOCALITY AND DISCUSSION. A single undistorted pedicle valve external mould (BB92215), length 6·0 mm, width 8·5 mm, depth 1·2 mm, was recovered from bed H6; two distorted brachial valves were also found (beds H6 and H40, BB92214). Only the pedicle valve specimen is figured. This is the earliest record of this species in the Lower Bala Group.

Fig. 24 ? *Lingulella* sp. (p. 202). Derfel Limestone, Nant Aber Derfel. BB92200a. Internal part of exfoliated pedicle valve, ×4·5.

Fig. 25 *Lingulella* cf. *ovata* (M'Coy) (p. 203). Gelli-grîn Formation, Rhiw March, Llanymawddwy. BB92201a. Internal part of exfoliated pedicle valve, ×4.

Figs 26–27 *Palaeoglossa* cf. *attenuata* (J. de C. Sowerby) (p. 203). Fig. 26, Gelli-grîn Formation, near Gelli-grîn Farm, Bala. BB92202. Articulated valves, ×3. Fig. 27, Cymerig Limestone Member, Rhiw March, Llanymawddwy. BB92203a. Internal part of exfoliated pedicle valve, ×3.

Fig. 28 ? *Pseudolingula* sp. (p. 203). Gelli-grîn Formation, near Gelli-grîn Farm, Bala. BB92204. External mould of a brachial valve, ×2.

Figs 29–30 *Paterula* sp. (p. 203). Cymerig Limestone Member, Rhiw March, Llanymawddwy. Figs 29a, b, BB92206. External mould of a pedicle (?) valve and latex cast of the same, both ×7·5. Fig. 30, BB92205. Internal mould of a pedicle valve, ×6.

Figs 31a, b *Orthisocrania* sp. (p. 205). Llaethnant Formation, Afon Twrch, near Bwlch y Groes. BB92207. Internal mould of a brachial valve, ×4; latex cast of same, ×5.

Figs 32a, b *Paracraniops* cf. *macellus* Williams (p. 203). Gelli-grîn Formation, near Gelli-grîn Farm, Bala. BB92208. Latex cast (a) of external mould of valve (b), both ×9.

Figs 33–36 *Paracraniops glaber* sp. nov. (p. 204). Allt Ddu Formation; all internal moulds. Figs 33–35, near Fedw Farm, Llangower. Fig. 33, **Holotype,** BB92209. Brachial (?) valve, ×6. Fig. 34, Paratype, BB92211. Brachial (?) valve, ×6. Fig. 35, Paratype, BB92210. Pedicle (?) valve, ×4. Fig. 36, Rhiw March, Llanymawddwy. Paratype, BB92212. Brachial (?) valve, ×6.

Fig. 37 *Paracraniops* cf. *glaber* Lockley (p. 205). Llaethnant Formation, Afon Twrch, near Bwlch y Groes. BB92213a. Internal mould of a brachial (?) valve, ×6.

Fig. 38 *Nicolella* cf. *actoniae obesa* Williams (above). Llaethnant Formation, Afon Twrch, near Bwlch y Groes. BB92215. External mould of a pedicle valve, ×3.

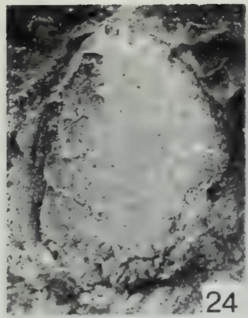
Fig. 39 *Rhactorthis crassa* Williams (p. 209). Nod Glas Formation, Rhiw March, Llanymawddwy. BB92216a. Internal mould of a brachial valve, ×3.

Fig. 40 *Howellites* cf. *ultimus* Bancroft (p. 209). Allt Ddu Formation, Rhiw March, Llanymawddwy. BB92217. External moulds of articulated valves, ×6.

Fig. 41 *Howellites* cf. *antiquior* (M'Coy) (p. 209). Ceiswyn Formation, Aber Cowarch, Dinas Mawddwy. BB92218a. Internal mould of a brachial valve, ×4.

Figs 42–43 *Onniella ostentata* Williams (p. 209). Llaethnant Formation, Afon Twrch, near Bwlch y Groes. Fig. 42, BB92219. Internal mould of a pedicle valve, ×3. Fig. 43, BB92220a. Internal mould of a brachial valve, ×3.

Fig. 44 *Salopia* sp. (p. 210). Llaethnant Formation, Afon Twrch, Bwlch y Groes. BB92222. Internal mould of a brachial valve, ×3.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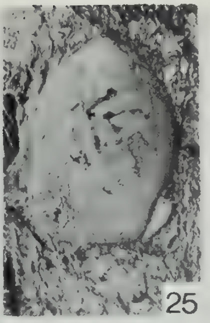
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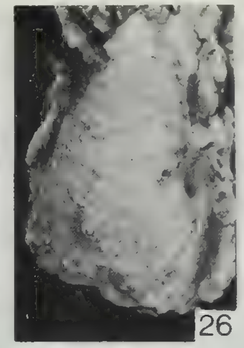
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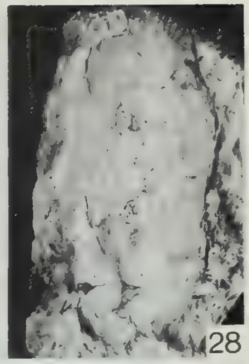
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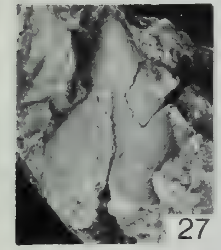
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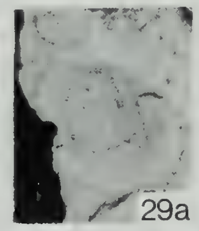
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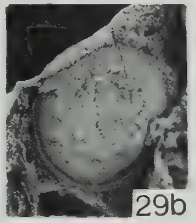
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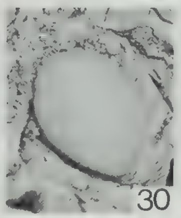
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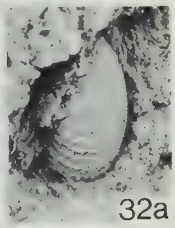
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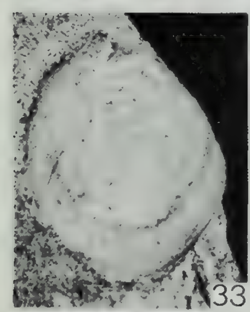
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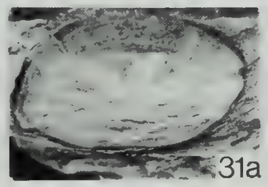
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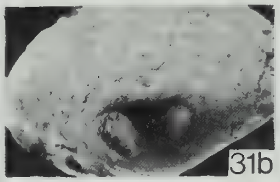
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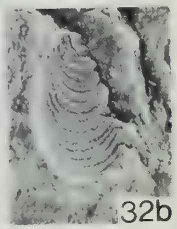
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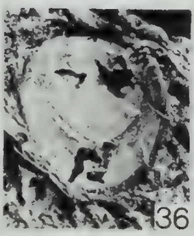
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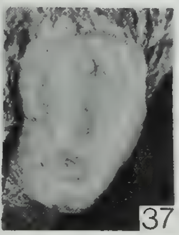
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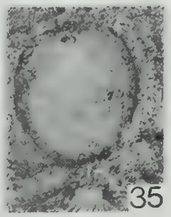
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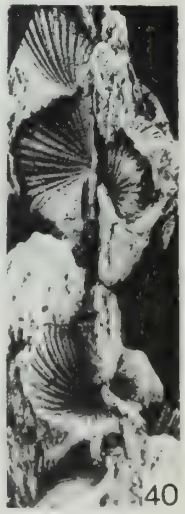
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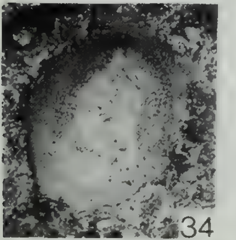
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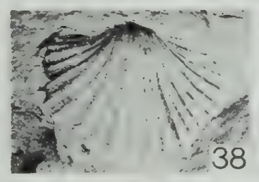
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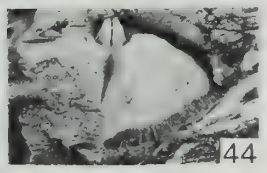
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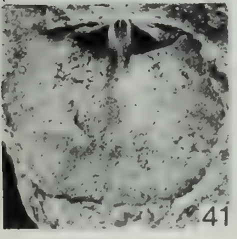
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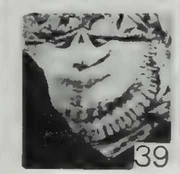
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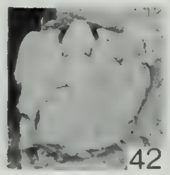
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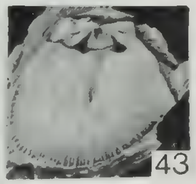
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A

	A	B
N	11	14
$\bar{l}$.mm(var.l)	2.827(0.522)	3.628(0.728)
$\bar{w}$.mm(var.w)	1.882(0.232)	2.443(0.359)
r	0.5996	0.8347
a(var.a)	0.666(0.032)	0.703(0.013)
$lg_e\bar{l}$(var.lg_el)	1.007(0.063)	1.262(0.054)
$lg_e\bar{w}$(var.lg_ew)	0.600(0.063)	0.864(0.058)
r_e	0.607	0.838
α (var.α)	1.000(0.70)	1.042(0.269)

C

A	B
12	7
4.00(1.453)	4.01(0.205)
3.65(1.319)	4.14(0.503)
0.9627	0.7301
1.343(0.087)	1.383(0.013)
1.247(0.094)	1.407(0.029)
0.9644	0.7326
1.0423(0.0076)	1.5123(0.212)

A Statistics of length (l) and maximum width (w) for Paracraniops glaber sp. nov. from horizons RO96 (A) and RO93 (B) in the Allt Ddu Mudstone at Rhiw March.

B Statistics of length (l) and width (w) of pedicle valves of Sericoidea abdita complicata subsp. nov. from four horizons (A-D) in the Nod Glas; (E-H) statistics of brachial valves from same samples.

C Statistics of length (l) and width (w) of pedicle (A) and brachial (B) valves of Cyclospira aff. bisulcata (Emmons) from the Cymerig Limestone and associated beds in the Tan y Bwlch and Rhiw March sections.

B

Locality	R 47	R 48	R 52	R 53	R 47	R 48	R 52	R 53
N	38	54	59	48	32	29	15	15
$\bar{l}$.mm(var.l)	2.54(0.289)	2.70(0.343)	2.476(0.468)	2.631(0.440)	2.38(0.273)	2.80(0.369)	2.26(0.395)	2.19(0.301)
$\bar{w}$.mm(var.w)	4.61(0.905)	5.06(1.866)	4.442(1.837)	4.9.5(2.157)	4.72(1.227)	5.04(1.501)	3.93(1.342)	4.61(1.357)
r	0.7429	0.8358	0.8341	0.8496	0.7395	0.8911	0.8242	0.9350
$lg_e.\bar{l}$(var.lg_e.l)	0.91(0.044)	0.974(0.046)	0.869(0.074)	0.936(0.062)	0.84(0.047)	1.01(0.046)	0.78(0.075)	0.75(0.061)
$lg_e.\bar{w}$(var.lg_e.w)	1.51(0.042)	1.587(0.070)	1.447(0.089)	1.549(0.085)	1.53(0.054)	1.59(0.058)	1.33(0.084)	1.50(0.062)
r_e	0.7470	0.8402	0.8397	0.8496	0.7444	0.8937	0.8299	0.9369
α (var.α)	0.975(0.012)	1.239(0.008)	1.099(0.006)	1.177(0.008)	1.07(0.017)	1.12(0.009)	1.06(0.027)	1.01(0.010)
	A	B	C	D	E	F	G	H

Fig. 45 Statistics for: A, *Paracraniops glaber* sp. nov. B, *Sericoidea abdita complicata* subsp. nov. C, *Cyclospira* aff. *bisulcata* (Emmons).

Family **PLECTORTHIDAE** Schuchert & Le Vene, 1929

Genus ***RHACTORTHIS*** Williams, 1963

Rhactorthis crassa Williams, 1963

Fig. 39

MATERIAL, LOCALITY AND DISCUSSION. Well-preserved, complementary internal and external moulds of a brachial valve (BB92216a, b) from bed R49 in the Rhiw March section; its length is 5·1 mm, width 7·0 mm.

Superfamily **ENTELETACEA** Waagen, 1884

Family **DALMANELLIDAE** Schuchert, 1913

Genus ***HOWELLITES*** Bancroft, 1945

Howellites cf. ***ultimus*** Bancroft, 1945 (emend. Williams 1963)

Fig. 40

MATERIAL, LOCALITY AND DISCUSSION. A group of at least seven articulated *Howellites* valves (BB92217) from bed R089 show attachment to an elongate strand of unknown material. The illustration of this specimen supplements descriptions of *Howellites* 'life assemblages' from the Berwyn area (Brenchley 1966).

Howellites cf. ***antiquior*** (M'Coy, 1852)

Fig. 41

MATERIAL, LOCALITY AND DISCUSSION. A well-preserved internal and external mould of a brachial valve (BB92218a, b), length 5·6 mm, width 7·0 mm, showing characteristic muscle scars, was recovered from bed AB07, associated with the Cowarch Phosphate Bed at Aber Cowarch.

Genus ***ONNIELLA*** Bancroft, 1928

Onniella ostentata Williams, 1963

Figs 42, 43

FIGURED MATERIAL. Representative internal moulds of a pedicle (BB92219) and a brachial valve (BB92220a) are shown.

HORIZON, LOCALITY AND DISCUSSION. Several populations of *O. ostentata* were recovered from beds H4–H7 and H38–H40 in Afon Twrch. The H4 population was compared with a population from bed GG1b at Gelli-grîn (type locality); no significant differences could be observed in the three allometrically controlled morphological features that were tested, the outline of the pedicle valve ($P > 10\%$), the outline of the brachial valve ($P > 10\%$) and the shape of the cardinalia ($10\% > P > 5\%$). (For statistics see Lockley 1977 : fig. 12.2). For a full description of this species see Williams (1963 : 405); it is discussed here to draw attention to its early appearance in pre-Frondderw beds.

Genus ***BANCROFTINA*** Sinclair, 1946

Bancroftina sp.

Figs 46a, b

MATERIAL, LOCALITY AND DISCUSSION. A well-preserved internal mould of a *Bancroftina* brachial valve (BB92221, length 13 mm, width 18 mm; cardinalia length 2·5 mm, width 5·5 mm) was recovered from bed GG1h above the Cymerig Limestone. This form is poorly represented in the Lower Bala Group.

Family **LINOPORELLIDAE** Schuchert & Cooper, 1931

Genus ***SALOPIA*** Williams, 1955

Salopia sp.

Fig. 44

Material, locality and discussion. This internal mould of a brachial valve (BB92222), from bed H6 below the Frondderw Ash, is one of several found in association with species which make an early appearance in the Lower Bala Group at about this horizon.

Suborder **TRIPLESIIDINA** Moore, 1952
Superfamily **TRIPLECIACEA** Schuchert, 1913
Family **TRIPLECIIDAE** Schuchert, 1913

Genus ***TRIPLESIA*** Hall, 1959

Triplesia maccoyana Davidson, 1869, emended

1852 *Hemithyris depressa* (J. de C. Sowerby); M'Coy *in* Sedgwick & M'Coy: 201.
1869 *Triplesia* ? *Maccoyana* Davidson: 199; pl. 24, fig. 29.
1978 *Triplesia*? *maccoyana* Davidson; Cocks: 86, 187.

Description. Small dorsibiconvex, globular, plicate *Triplesia* with pedicle valve averaging 96% as long as wide in 5 specimens (range 80–108%) and 22% as deep as long in 4 specimens (range 15–27%); dorsal valve averaging 87% as long as wide in 13 specimens and 45% as deep as long in 12 specimens; ventral sulcus and corresponding dorsal fold arising between the 2 and 3 mm growth stages and averaging 62% as wide (wavelength) as valve (range 56–67%) and 30% as high (amplitude) as wavelength (range 21–40%) at the commissure of 4 smaller valves between 3·6 and 5·0 mm in width, deepening to respective average width : wavelength and amplitude : wavelength ratios of 59% (range 55–63%) and 44% (range 39–47%) at the commissure of 4 larger valves between 5·5 and 7·2 mm in width; ventral umbo pointed, overhanging incurved dorsal umbo and with short narrow curved apsacline interarea divided by elongate pedicle groove; surface smooth except for fine concentric growth lines numbering about 10 per mm beyond the 3 mm growth stage. Interior of both valves unknown.

Material and locality. Lectotype (selected Cocks 1978: 86) articulated valves (SMA.42436), length 5·6 mm, width 7·0 mm, and 19 other paralectotypes (SMA.42437–48) from a limestone lens in the Allt Ddu Mudstones, Bryn Bedwog Quarry, near Bala, Gwynedd (grid. ref. SH 931329).

Discussion. The species is known only from M'Coy's original material and its importance as an element of the Lower Bala Group fauna is difficult to evaluate. It is, however, the first *Triplesia* species recorded in the Ordovician of north Wales; Williams (1974) recorded a contemporary *Triplesia* sp. from the Soudleyan of Salop. There is also an earlier species, *Triplesia edgelliana* (Davidson), from the Upper Llanvirn of the Llandeilo area (Lockley & Williams, in press); *T. maccoyana* compares most closely with this, differing only in respect of its significantly deeper dorsal valve ($0{\cdot}05 < P < 0{\cdot}02$). Relevant statistics for the dorsal valve length (l), width (w) and depth (th) are as follows: ($n = 13$) $\bar{l}$ mm (var. l) 5·14 (1·273), $\bar{w}$ mm (var. w) 5·91 (2·185), $r = 0{\cdot}9077$, a (var. a) 1·3103 (0·0275); ($n = 12$) $\bar{l}$ mm (var. l) 5·32 (0·938), $\overline{th}$ (var. th) 2·42 (0·552), $r = 0{\cdot}8066$, a (var. a) 0·7675 (0·0206).

Order **STROPHOMENIDA** Öpik, 1934
Superfamily **PLECTAMBONITACEA** Jones, 1928
Family **LEPTESTIIDAE** Öpik, 1933
Subfamily **LEPTESTIINAE** Öpik, 1933

Genus ***PALAEOSTROPHOMENA*** Holtedahl, 1916

Palaeostrophomena canalis sp. nov.

Figs 47a, b, 48–52

Diagnosis. Subquadrate, gently biconvex to biplanate *Palaeostrophomena* with pedicle valve characterized by well-developed mantle canal system arising anteromedially and restriction of genital markings to posterolateral part of valve.

NAME. With reference to the mantle canal system.

DESCRIPTION. Pedicle valve 85–90% as long as wide with interior characterized by elongate, narrow, divergent diductor scars flanking narrow, small anterior median adductor scars. Musculature otherwise poorly defined and intricately related to well-defined mantle canal system.

Interarea long apsacline, dental lamellae absent, but divergent false dental plates present. Narrow delthyrium open medially but covered laterally by pseudodeltidium. Up to 12 mantle canals branching radially into at least 30 tributary canals at the commissure. At least seven concentric rugae (wavelength 0·2 mm) developed posterolaterally at an acute angle to the hinge. Ornament very fine, unequally parvicostellate; at least seven ribs arise in umbonal area defining sectors bisected by ribs arising 3–4 mm from umbo, and these in turn define sectors bisected by ribs arising 5–6 mm from umbo. Brachial valve unknown.

TYPE MATERIAL. Measurements in mm.

	length	width
Holotype, internal mould of pedicle valve, BB92223 . . .	(15)	(16·5)
Paratype, internal mould of pedicle valve, BB92224 . . .	(13)	(18)
Paratype, internal mould of pedicle valve, BB92225 . . .	(12)	(12)
Paratype, internal mould of pedicle valve, BB92226 . . .	(9)	(12)
Paratype, internal mould of pedicle valve, BB92227 . . .	(9)	(15)
Paratype, external mould of pedicle valve, BB92228 . . .	(9)	(11)

TYPE HORIZON AND LOCALITIES. Holotype from sample GG1b in the Gelli-grîn type section; paratypes from samples R27 and R28 in the Rhiw March section.

DISCUSSION. This species is quite distinct from *P. magnifica* Williams, which is known from the Derfel Limestone. The lack of well-developed genital markings and the closely-spaced mantle canals are its most distinctive features. Cooper (1956 : 703) noted the complete absence of well-preserved brachial valves in a large population of *P. angulata* and attributed this to their fragility. Although similar absence of brachial valves of *P. canalis* is noted here, explanations are not proposed.

Family **SOWERBYELLIDAE** Öpik, 1930

Subfamily **SOWERBYELLINAE** Öpik, 1930

Genus ***ANISOPLEURELLA*** Cooper, 1956

Anisopleurella cf. ***multiseptata*** (Williams, 1955)

Fig. 53

DISCUSSION. A well-preserved specimen of a pedicle valve internal mould (BB92229) from bed GG2b represents the first record of *Anisopleurella* in the Gelli-grîn Formation. The large, paired diductor scars are well displayed and the fragmentary remains of external moulds which were also recovered reveal the essentially smooth exterior of the shell which is ornamented only by widely-spaced primary costae. The specimen compares closely with *A. multiseptata* Williams from the Derfel Limestone (Williams *in* Whittington & Williams 1955 : 416).

Subfamily **AEGIROMENINAE** Havlíček, 1961

Genus ***SERICOIDEA*** Lindström, 1953

Sericoidea abdita Williams, 1955, emend. herein

DIAGNOSIS. *Sericoidea* with variable arrangement of paired or single strong lateral septules and a well-defined median septum all extending into the anterior half of the valve; dorsal muscle platform bilobed.

Sericoidea abdita complicata subsp. nov.
Figs 54–59

DIAGNOSIS. Differs only from the nominate subspecies in the variable development of septules and the presence of dorsal muscle scars.

NAME. 'Complicated'.

DESCRIPTION. Semicircular, planoconvex *Sericoidea* with mean length/width ratio of 54·4% and 52·7% for pedicle (N = 199) and brachial (N = 91) valves respectively. Ornamentation consisting of fine, differentially thickened, radial costae and costellae with a mean of 12·4 per mm (N = 56) found anteromedially. Dorsal septules arranged in arcs over two-thirds of the length of the brachial valve anterior of the umbo. Septules are generally but not invariably arranged in arcuate, single or double rows, or both, on either side of the median septum. The mean number of septules per row (as counted for the longest row) is 5·8 (N = 25). Dorsal adductor scar bilobed, extending anteriorly for less than half the length of the valve and laterally for over one-third the width of the valve.

TYPE MATERIAL. Measurements in mm.

	length	width
Holotype, internal mould of brachial valve, BB92231 . . .	5·0	2·8
Paratype, internal mould of brachial valve, BB92230 . . .	–	–
Paratype, exterior of pedicle valve, BB92232	5·3	3·5
Paratype, exterior of pedicle valve, BB92233	4·6	3·0
Paratype, internal mould of brachial valve, BB92234 . . .	–	–
Paratype, internal mould of brachial valve, BB92235 . . .	5·0	3·2
Paratype, exterior of pedicle valve, BB92236	7·0	4·0

TYPE HORIZON AND LOCALITY. Nod Glas Formation, Rhiw March: holotype from bed R47 and paratypes from beds R52 and R53.

DISCUSSION. The genus *Sericoidea* is abundantly represented in the Nod Glas. The largest populations were recovered from beds R47, R48, R52 and R53; full statistical details are given in Fig. 45B. Estimates of α, the growth ratio for samples affected by allometry, have been derived from the data in Fig. 45B and tests show that none of the populations differs significantly from any other ($P > 0{\cdot}1$). Furthermore, they do not differ significantly from *S. restricta* from the Sulårp Shale and from *S.* aff. *restricta* from the Craighead Limestone; nor do they differ significantly from *S.* aff. *abdita* from the Balclatchie Mudstones either at Laggan Burn or Byne Hill ($P > 0{\cdot}1$, for all tests). Even when using growth ratios not corrected for allometry, no significant difference

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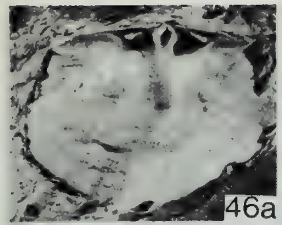
Figs 46a, b *Bancroftina* sp. (p. 209). Gelli-grîn Formation, Gelli-grîn Farm, Bala. BB92221. Internal mould and latex cast of a brachial valve, both ×2·5.

Figs 47–52 *Palaeostrophomena canalis* sp. nov. (p. 210). Gelli-grîn Formation. Figs 47a, b, Gelli-grîn Farm, Bala. **Holotype,** BB92223. Internal mould and latex cast of a pedicle valve, ×2·5. Figs 48–52, Rhiw March, near Llanymawddwy. Figs 48–50, Paratypes, BB92226, BB92225, BB92227. Internal moulds of pedicle valves, all ×2. Fig. 51, Paratype, BB92224. Internal mould of a pedicle valve, ×2·5. Fig. 52, Paratype, BB92228. External mould of a pedicle valve, ×2·5.

Fig. 53 *Anisopleurella* cf. *multiseptata* (Williams) (p. 211). Gelli-grîn Formation, Maes-Meillion, near Llangower. BB92229. Internal mould of a pedicle valve, ×2·5.

Figs 54–59 *Sericoidea abdita complicata* subsp. nov. (above). Nod Glas Formation, Rhiw March, Llanymawddwy. Fig. 54, **Holotype,** BB92231. Internal mould of a brachial valve, ×7·5. Figs 55–57, Paratypes, BB92230, BB92235, BB92234. Internal moulds of brachial valves, ×12, ×6 and ×7·5 respectively. Figs 58–59, Paratypes, BB92233, BB92232. Exteriors of pedicle valves, both ×6.

Figs 60–62 *Bimuria dyfiensis* sp. nov. (p. 215). Gelli-grîn Formation, Rhiw March, near Llanymawddwy. Figs 60–61, internal moulds of pedicle valves, ×2·5. Fig. 60, **Holotype,** BB92237. Fig. 61, Paratype, BB92239a. Figs 62a, b, Paratype, BB92238a. Posterior and lateral views of a pedicle valve, both ×2·5. See also Figs 64–65.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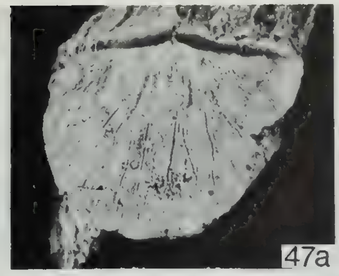
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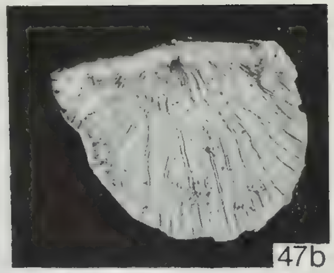
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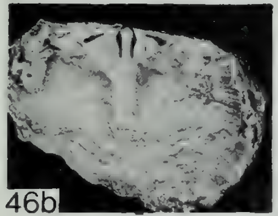
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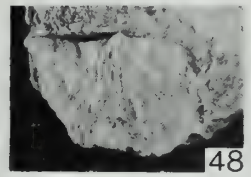
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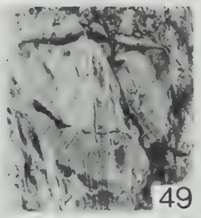
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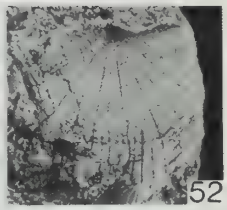
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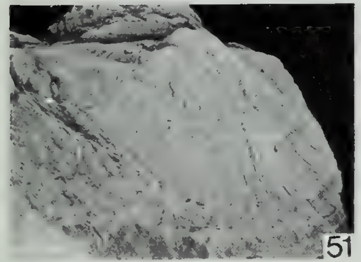
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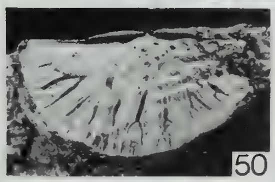
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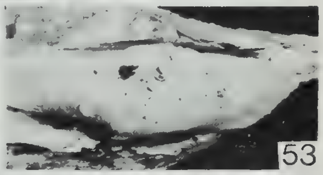
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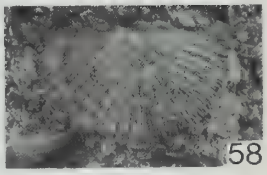
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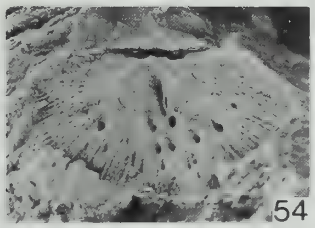
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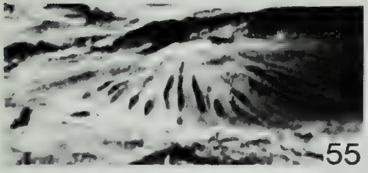
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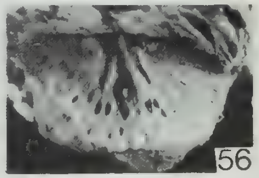
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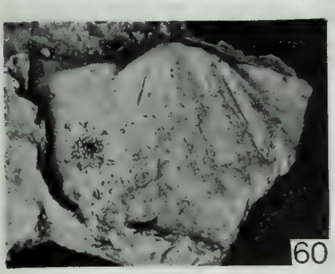
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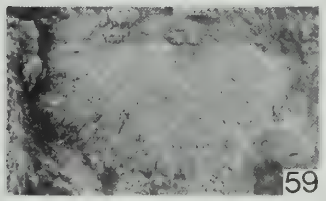
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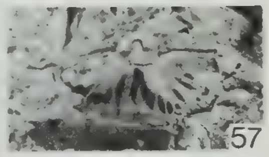
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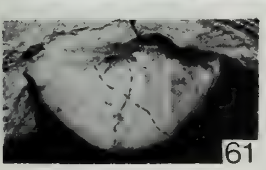
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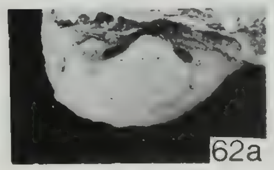
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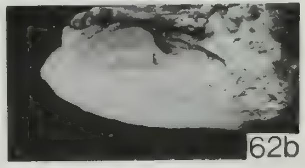

62b

A

9	10	11	12	13	14	15	16	17	18	19	costellae per mm
-	5	6	15	6	13	6	2	2	1	-	N

B

costellae per mm.	9-11	12	13-18	N	
	5	16	41	62	S. aff. abdita
	11	15	30	56	S. abdita complicata

C

	MS	1	2	3	4	5	6	7	8	9	10	
0·6 - 1·0	-(3)											- (3)
1·1 - 1·5	-(1)	1(1)				2(-)						3 (2)
1·6 - 2·0		-(2)	1(-)	-(4)	1(-)	2(-)	1(-)	1(-)				6 (6)
2·1 - 2·5		-(2)		-(3)	1(-)	1(-)	3(-)	4(-)				9 (5)
2·6 - 3·0				-(4)		1(-)	2(-)	2(-)			1(-)	6 (4)
3·1 - 3·5				-(3)						1(-)		1 (3)
	-(4)	-(5)	1(-)	-(16)	2(-)	6(-)	6(-)	7(-)	--	1(-)	1(-)	24(25)

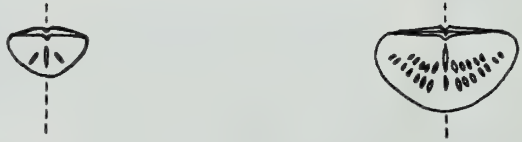


Fig. 63 A, frequency of counts of costellae per mm occurring at the anteromedian margins of *Sericoidea abdita complicata* subsp. nov. B, pooled data for costellae frequency in *S.* aff. *abdita* from Laggan Burn and Byne Hill and in *S. abdita complicata* subsp. nov. C, the distribution of various types of lophophore platforms, with from 1 to 10 septules either side of the median septum (MS) in *S.* aff. *abdita* from Laggan Burn (number of individuals in brackets) and *S. abdita complicata* subsp. nov. from the Nod Glas (number of individuals not in brackets).

can be detected between *S. abdita complicata* and *Chonetoidea radiatula* (Barrande) from the Ashgill of Pomeroy ($P > 0{\cdot}1$). This evidence highlights the similarity in the shape of these related aegiromeninids.

Williams (1963 : 188–190) measured the frequency of costellae per mm at the anteromedian margins of *Sericoidea* and found that *S.* aff. *abdita* from the Balclatchie Mudstones was significantly different from S. aff. *restricta* from the Craighead Limestone. In this study similar measurements on the frequency of costellae at the anteromedian margin in *S. abdita complicata* were compared with measurements obtained for *S.* aff. *abdita*, using a χ^2 test with cell groupings identical to those used by Williams (1963 : 189). No significant difference was detected between the two populations ($0{\cdot}2 > P > 0{\cdot}1$); the data are given in Fig. 63.

However, a comparison between the different types of septule arrangement in *S.* aff. *abdita* and *S. abdita complicata* reveals that the latter subspecies was significantly different (χ^2 test, $P < 0{\cdot}001$) in having longer rows of single and paired septules of comparable size; see Fig. 63.

Since there is a high degree of variability in the disposition of septules in the *S. abdita complicata* population the differences are considered subspecific.

Although attempts have been made by Williams (1962) and the author to define *Sericoidea* populations quantitatively, a certain element of qualitative judgement attaches to whether smaller or larger septules are considered important as representatives of well-defined or less well-defined rows. According to Williams (1962 : table 46) septule rows never contain more than three septules (either in *S. restricta* or in *S.* aff. *abdita*). Similarly, *S. abdita* was diagnosed as having 'up to three pairs of strong lateral septules' (Williams *in* Whittington & Williams 1955 : 418). However, whilst acknowledging that palaeontologists might differ as to what constitutes a septule rather than a tubercle (the specimens in Williams 1974 : pl. 24, figs 8, 9 and Williams 1962 : pl. 18, fig. 8 might for example be considered to display at least four septules in each lateral row) the differences between *S.* cf. *abdita*, S. aff. *abdita* and *S. abdita complicata* are considered significant because all measurements and counts of morphological features were estimated in the same way.

Family **BIMURIDAE** Cooper, 1956

Genus ***BIMURIA*** Ulrich & Cooper, 1942

Bimuria dyfiensis sp. nov.

Figs 60, 61, 62a, b, 64a, b, 65

DIAGNOSIS. Concavo-convex, small, slightly sulcate *Bimuria* with pedicle valve umbo strongly incurved and overlapping dorsal interarea, teeth simple.

NAME. From the Dyfi river.

DESCRIPTION. The pedicle valve interior morphology is well defined. Variably developed, narrow, divergent diductor scars extend anterolaterally for approximately three-quarters of the length of the valve, enclosing less well defined, radial adductor and mantle canal impressions posteromedially. Simple teeth developed laterally for about one-third of the width of the valve but short anteromedially. Slight development of pedicle valve sulcus evident from broad indentation of anterior commissure.

Brachial valve interior unknown; exterior essentially smooth in the only known specimen. Ventral exterior poorly known, essentially smooth, comae absent or very indistinct, resembling faint concentric growth lines where present.

TYPE MATERIAL, HORIZON AND LOCALITY. Holotype, internal mould of pedicle valve (BB92237) from bed R28 (length 12 mm, width 16 mm). Paratypes, internal and external moulds of pedicle valves (BB92238a, b–BB92241a, b) and internal moulds of pedicle valves (BB92242 and BB92243) and a brachial valve (BB92244), all from bed R28.

The above specimens, all from bed R28 in the Gelli-grîn Formation at Rhiw March, are distorted so that measurements are inaccurate; but the mean size of this population was clearly small, only two specimens being slightly wider than 12 mm.

DISCUSSION. The morphological features described above suggest that this species cannot be assigned to any of the Scoto-Irish species (*B.* cf. *buttsi* Cooper, *B. youngiana* Davidson, *B. youngiana recta* Williams and *B.* cf. *youngiana recta*). The Welsh specimens apparently belonged to a population with a smaller mean size than the two former Scoto-Irish species populations (and the latter subspecies population). More significantly, however, the lack of any comae or other distinctive concentric ornamentation must be regarded as an important morphological difference. This lack of ornamentation is not simply the result of the small size of the Welsh specimens; Williams (1962 : 174–175) reported comae originating at 4–6 mm from the ventral umbo in all three of the Scottish species he described. Although the length of the Welsh specimens is not determined precisely, if one can assume, following Williams (1962) and Mitchell (1977), that *Bimuria* is at least two-thirds to three-quarters as long as wide, then all the Welsh specimens must be 6 mm or more in length. *B. dyfiensis* represents the first known occurrence of the genus *Bimuria* in Wales; since it is morphologically distinct, in respect of its essentially smooth external ornament, from all other known species in Britain, it is given specific recognition.

Order **PENTAMERIDA** Schuchert & Cooper, 1931
Suborder **SYNTROPHIIDINA** Ulrich & Cooper, 1936
Superfamily **PORAMBONITACEA** Davidson, 1853
Family **PARASTROPHINIDAE** Ulrich & Cooper, 1938

Genus ***PARASTROPHINELLA*** Schuchert & Cooper, 1931

Parastrophinella brenchleyi sp. nov.
Figs 66–69

DIAGNOSIS. Large, subpentagonal, biconvex *Parastrophinella* with vestigial fold and sulcus and commonly 12 costae, with a wavelength of 1·0–1·5 mm, ornamenting anteromedian part of the shell.

NAME. For Dr P. J. Brenchley.

DESCRIPTION. Unequally biconvex, rostrate *Parastrophinella* with a subpentagonal outline. 80% as long as wide with pedicle valve about 30% as deep as long. Transverse profile convex with steep lateral slopes; longitudinal profile unevenly convex to anteriorly geniculate in larger specimens. Faintly and sporadically developed low dorsal fold with at least 4 costae and shallow ventral sulcus with 3 costae. Twelve variably developed ventral costae are characteristically angular and well developed anteromedially (being 1·0–1·5 mm in width and amplitude) but are rounded and indistinct posterolaterally. Variably developed concentric corrugations up to 4 per mm anteromedially and anterolaterally are faint or absent in posteromedian part of shell.

Ventral interior with spondylium which is sessile posteriorly but supported anteriorly by sporadically developed medium septum extending forward for an average of 49% of the length of three pedicle valves. Muscle scars very faint or absent. Dorsal interior unknown.

TYPE MATERIAL. Measurements in mm.

	length	width
Holotype. Internal mould of a pedicle valve, NMW 77.11G.24	(10·0)	(15·0)
Paratype. Internal mould of a pedicle valve, NMW 77.11G.25	(7·0)	(9·0)
Paratype. Internal mould of a pedicle valve, NMW 77.11G.26	(10·5)	(10·5)
Paratype. Internal mould of a pedicle valve, NMW 77.11G.27	(9·0)	(11·0)
Paratype. Internal mould of a pedicle valve, NMW 77.11G.28	–	–

(Measurements given here indicate respective mean length and width values of 9·12 and 11·37 mm)

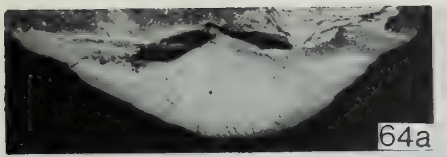
TYPE HORIZON AND LOCALITY. Bryn Beds (Lower Longvillian) exposed in small overgrown quarry 55 m east of Pandy Quarry (SJ 202363).

Figs 64–65 *Bimuria dyfiensis* sp. nov. (p. 215). Gelli-grîn Formation, Rhiw March, near Llanymawddwy. Figs 64a, b, Paratype, BB92241a. Internal mould of a pedicle valve, ×4; corresponding latex cast, ×2·5. Fig. 65, Paratype, BB92240a. Internal mould of a pedicle valve, ×4. See also Figs 60–62.

Figs 66–69 *Parastrophinella brenchleyi* sp. nov. (above). Bryn Beds, Pandy Quarry, near Glyn Ceriog. Fig. 66, **Holotype**, NMW.77.11G.24. Internal mould of a pedicle valve, ×4. Figs 67–69, Paratypes, NMW.77.11G.26, NMW.77.11G.25 and NMW.77.11G.27 respectively. Internal moulds of pedicle valves, all ×4.

Figs 70–76 *Protozyga musculosa* sp. nov. (p. 218). Nod Glas Formation; all internal moulds. Figs 70, 74–76, Rhiw March, near Llanymawddwy. Fig. 70, Paratype, BB92249. Pedicle valve, ×8. Fig. 74, Paratype, BB92246. Pedicle valve, ×16. Fig. 75, Paratype, BB92252. Brachial valve, ×10. Fig. 76, Paratype, BB92247. Pedicle valve, ×16. Figs 71–73, Nant Tan y Bwlch, near Bwlch y Groes. Fig. 71, Paratype, BB92253. Pedicle valve, ×9. Fig. 72, **Holotype**, BB92245. Pedicle valve, ×12. Fig. 73, Paratype, BB92254. Pedicle valve, ×9.

Figs 77a, b *Cyclospira* aff. *bisulcata* (Emmons) (p. 219). Cymerig Limestone Member, Rhiw March, near Llanymawddwy. BB92255. Ventral and dorsal views of the exterior of an articulated specimen, both ×6. See also Figs 78–82.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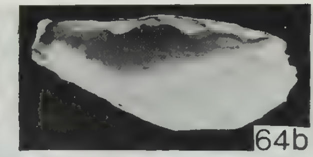
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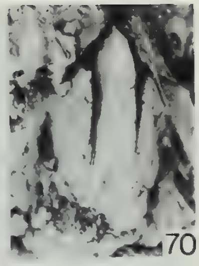
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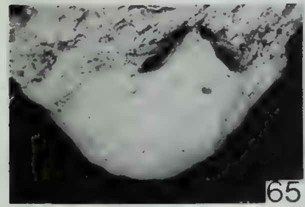
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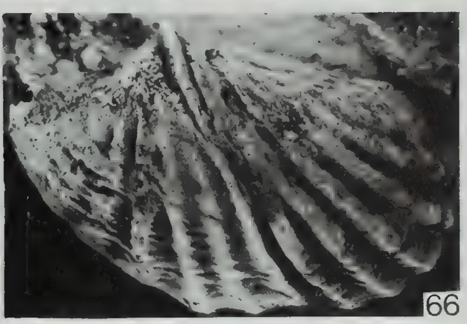
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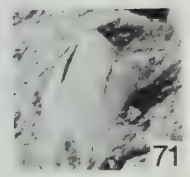
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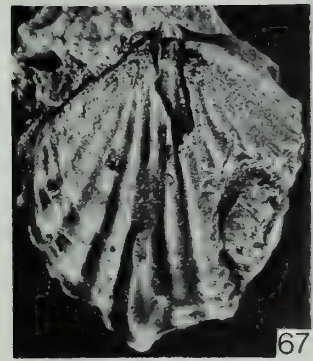
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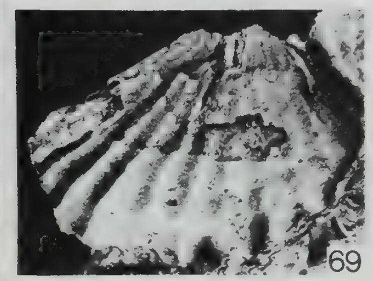
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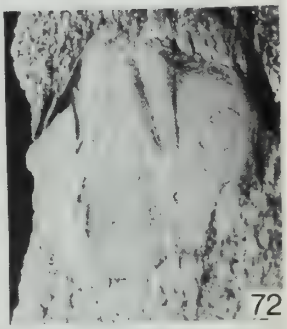
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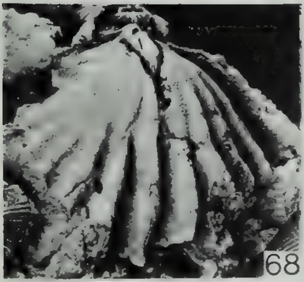
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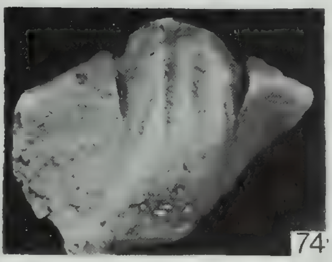
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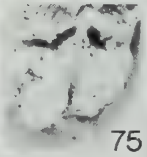
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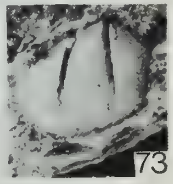
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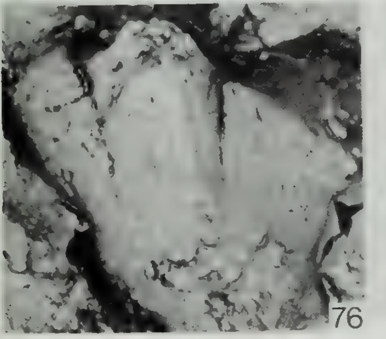
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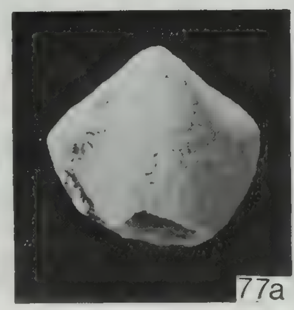
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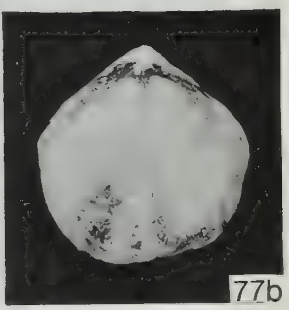

77b

Discussion. This material, collected by Dr P. J. Brenchley from a single locality, has hitherto been described only briefly and informally (Brenchley 1966 : 242; figs 161–162). *Parastrophinella* is known from Scotland (Williams 1962), from Wales (MacGregor 1961, Addison 1974) and from the Welsh Borderland (Williams 1974). The Scottish species *P. youngi* (Reed) from the Craighead Limestone (Caradoc) differs from *P. brenchleyi* in being characteristically tumid with poorly-developed costae primarily associated with plication. Similarly, *P. parva* MacGregor (1961 : 197) from the Llandeilo rocks of the Berwyns is small, tumid and lacks well-developed costae; Addison (1974 : 47) also recorded this species in rocks of early Caradoc age near Narbeth (Pembrokeshire). However, the other smaller species, *P. costata* MacGregor (1961 : 199) from the Llandeilo of the Berwyns, resembles *P. brenchleyi* in outline, length/width ratio and spondylial arrangement, but differs in being considerably smaller (mean size) and having a larger number of costae (13–22). *P. musculosa* Williams (1974 : 151) from the Spy Wood Grit, Salop, resembles *P. brenchleyi* sp. nov. in 'commonly' having 11–13 costae (mean *c.* 12) and exhibiting a poorly-developed fold and sulcus and a similar spondylial arrangement; however, it differs in being smaller than *P. brenchleyi* (55% of mean width) and relatively but not significantly wider ($25 > P > 10$). A mean width/length ratio of 0·93 for 4 brachial valves of *P. musculosa* implies a smaller value for the corresponding, relatively longer pedicle valves (say $< 0{\cdot}90$); this differs considerably from the ratio of 1·25 for 4 pedicle valves of *P. brenchleyi*. Although allometric growth might account for a relative increase in width with size, even in the absence of more material the differences in size, shape and ornament between *P. musculosa* and *P. brenchleyi* are sufficient to merit the systematic recognition of the latter species. Williams (1974 : 152) also described *Parastrophinella* sp. from the Hagley Volcanics; although resembling *P. brenchleyi* in its sub-pentagonal outline and large size it differs from this form in having about 20 well-developed costae.

Order **SPIRIFERIDA** Waagen, 1883
Superfamily **ATRYPACEA** Gill, 1871
Family **ATRYPACEA** Gill, 1871

Genus ***PROTOZYGA*** Hall & Clarke, 1893

Protozyga musculosa sp. nov.
Figs 70–76

Diagnosis. Small subcircular to subspherical *Protozyga* with well-developed dental plates and pedicle valve musculature.

Name. With reference to the well-developed musculature.

Description. Small subcircular to subeliptical or subpentagonal ventribiconvex *Protozyga* as wide as long, with long subparallel to slightly divergent dental plates extending anteromedially for between half and two-thirds the length of the pedicle valve and enclosing equally long diductor muscle scars best developed in larger specimens. External features poorly known; ornamentation smooth but nature of anterior arc of commissure unknown.

Brachial valve interior with posterolateral socket plates and long median septum arising at a point anterior to the hinge line and extending anteriorly for most of the length of the valve.

Statistics for three measured pedicle valve paratypes; mean length (2·73 mm), mean width (2·73), r (0·9736), a (1·077) and b (−0·1415).

Type material, horizon and localities. Holotype, internal mould of pedicle valve, BB92245 (length 3 mm, width 3 mm). From bed TB19 in the Nod Glas at Nant Tan y Bwlch. Paratypes, internal moulds of pedicle valves, BB92246–BB92251 and BB92253–BB92254, and a single brachial valve, BB92252. From beds TB19 and R54 in the Nod Glas at Rhiw March.

Discussion. This occurrence is the first record of *Protozyga* in Wales; related forms including *P. diversa* (Reed), *P. rotunda* Cooper and *P. perplexa* Williams from Girvan and *P.* cf. *perplexa* and *P.* cf. *diversa* from Pomeroy are unlike the Welsh species both in the ventral arrangement of dental plates and diductor muscle scars and in the posterior origin of the brachial valve median septum.

Superfamily **DAYIACEA** Waagen, 1883
Family **DAYIIDAE** Waagen, 1883
Subfamily **CYCLOSPIRINAE** Schuchert, 1913
Genus ***CYCLOSPIRA*** Hall & Clarke, 1893
Cyclospira aff. ***bisulcata*** (Emmons, 1842)
Figs 77–82

DIAGNOSIS. Unequally biconvex, subpentagonal *Cyclospira* with rounded anterior margin.

DESCRIPTION. Unequally biconvex *Cyclospira* with pedicle valve nine-tenths as wide as long and brachial valve about as wide as long. Pedicle valve strongly convex in median part of valve with slight development of anteromedian sulcus and flat or concave posterolateral flanks or 'wings' subparallel to commissural plane.

External ornament mainly smooth but with fine concentric growth lines developed anteriorly and fine radial striations emphasized by slight exfoliation of shells. Pedicle interior characterized by well-developed 'shoelifter process' partly anterior to ventral muscle field.

Brachial valve sulcate with slight development of median plication dividing anterior part of sulcus. Interior characterized by median septum originating just anterior of medially cleft hinge line and extending anteriorly for at least three-quarters of the valve length. Thin socket plates present.

MATERIAL. Measurements in mm.

	PV		BV	
	length	width	length	width
Complete articulated specimen, BB92255	5·0	5·5	4·5	5·5
Complete articulated specimen, BB92256	4·0	3·5	3·9	3·5
External of pedicle valve, BB92257	5·6	5·0	–	–
Latex cast of articulated specimen, BB92258	4·6	4·4	4·2	4·4
Complete articulated specimen, BB92259	4·7	4·6	4·1	4·6
Internal and external mould of pedicle valve, BB92260a, b	(5·0)	(4·2)	–	–
Internal mould of brachial valve, BB92261	–	–	–	(3·0)

Statistics of length and width for 12 pedicle and 7 brachial valves are given in Fig. 45C.

HORIZON AND LOCALITIES. From bed R53 in the Cymerig Limestone at Rhiw March and bed TB20 in the Tan y Bwlch section.

DISCUSSION. The material recovered in this study affords an excellent opportunity to elaborate on the description of the *Cyclospira* sp. which Williams (1963 : 469) described as 'reminiscent' of *C. bisulcata* (Emmons). *C. bisulcata* is one of six species described by Cooper (1956); of these only a form related to *C.* ? *longa* (Cooper) has previously been described from British successions (Williams 1962 : 251; pl. 23). *C. carrickensis* (Reed) and *C. nana* (Davidson) have also been described from Ordovician rocks by Williams (1962) and Mitchell (1977) respectively. The specimens from north Wales are unlike *C.* ? *longa*, which has an almost triangular outline with incipient plication of the anterior commissure (Cooper 1956 : pl. 142.I). They are also unlike *C. nana* in having a longer median septum and thinner socket plates. They differ from *C. carrickensis* in not having an emarginate anterior commissure (Williams 1962 : 250) but are otherwise similar in exterior morphology.

The present *C.* aff. *bisulcata* bears a general resemblance to both *C. quadrata* Cooper and *C. preciosa* Cooper, but these two American species lack any median plication in the dorsal sulcus and show little or no ventral sulcation. *C. parva* Cooper and particularly *C. sulcata* Cooper are considerably more elongate than the present form. The species described by Cooper are hard to differentiate on external morphology; internal features are not illustrated, though *C. parva*, *C. quadrata* and *C.* ? *longa* are all known to have a dorsal median septum. The species based on British specimens (including *C.* aff. *bisulcata*) are probably better known in their internal morphology. The designation of this species as *C.* aff. *bisulcata* supports the suggestion of Williams (1963) that the Welsh Cyclospiridae belong to a group closely related to *C. bisulcata*.

Superfamily unknown

? **Spiriferide**, gen. indet.

Fig. 83

Description and discussion. Pedicle valve about as wide as long, with well-defined 'shoelifter process', which differs from *C.* aff. *bisculcata* in having paired raised scars in median part of valve between flanks of anterior part of process. External ornament of (unfigured) counterpart smooth. Posterior lateral flanks of valves show more 'wing-like' extension than in *C.* aff. *bisulcata*, but the possibility that this specimen is closely related to that form cannot be ruled out.

Material and locality. Pedicle valve internal and external moulds (BB92262a, b), from loc. 615a in beds above the Cymerig Limestone on Pen y Cefn Coch.

Other phyla

In addition to the brachiopod taxa described above, representatives of other phyla, notably the Arthropoda (Trilobita) and Mollusca (Bivalvia), are also recorded in the Lower Bala Group for the first time. These include four trilobite genera and five bivalve genera which are figured below but not accompanied by full systematic descriptions. Brief discussion on the significance of these newly recorded genera is included where appropriate.

Phylum **ARTHROPODA** Siebold & Stannius, 1845

Class **TRILOBITA** Walch, 1771

Family **PHILLIPSINELLIDAE** Whittington, 1950

Genus ***PHILLIPSINELLA*** Novak, 1886

Phillipsinella sp.

Figs 84–87

Material and locality. Three pygidia (It.14294–6) and four cephalic (glabellar) fragments (It.14297–300) from bed R53 in the upper part of the Cymerig Limestone at Rhiw March.

Discussion. These specimens, from beds of 'presumed' Upper Longvillian age, are the oldest known *Phillipsinella* specimens in Britain (Ingham, personal communication 1977); they are the first record of this genus in the Caradoc Series of north Wales. The phylogeny of the genus is discussed in Bruton (1976).

Figs 78–82 *Cyclospira* aff. *bisulcata* (Emmons) (p. 219). Figs 78–81, Cymerig Limestone Member, Rhiw March, near Llanymawddwy. Fig. 78, BB92258. Posterodorsal view of latex cast of an articulated specimen, ×7·5. Fig. 79, BB92257. Exterior of a pedicle valve, ×5. Fig. 80, BB92261. Internal mould of a brachial valve, ×8. Figs 81a, b, BB92256. Ventral and dorsal views of the exterior of a broken articulated specimen, both ×5. Fig. 82, Nod Glas Formation, Nant Tan y Bwlch, near Bwlch y Groes. BB92260. Internal mould of a pedicle valve, ×5. See also Figs 77a, b.

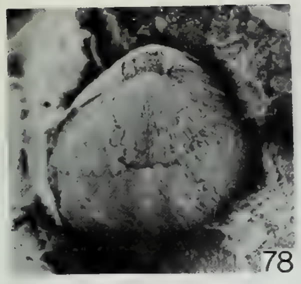
Fig. 83 ? Spiriferide, gen. indet. (above). Gelli-grîn Formation, Pen y Cefn Coch. BB92262a. Internal mould of a pedicle valve, ×5.

Figs 84–87 *Phillipsinella* sp. (above). Cymerig Limestone, Rhiw March, near Llanymawddwy. Figs 84a, b, It.14297. Oblique left-lateral and left-lateral views of a cranidium, ×16. Fig. 85, It.14298. Oblique left-lateral view of a cranidium, ×16. Fig. 86, It.14299. Dorsal view of a small cephalon, ×15. Fig. 87, It.14294. Dorsal view of a pygidium, ×16.

Figs 88–89 *Lonchodomas* sp. (p. 222). Cymerig Limestone Member, Rhiw March, near Llanymawddwy. Fig. 88, It.14301. Dorsal view of plasticine cast of cranidium, ×3. Fig. 89, It.14302. Dorsal view of cranidium, ×4.

Figs 90–91 *Sphaerocoryphe* sp. (p. 222). Cymerig Limestone Member, Rhiw March, near Llanymawddwy. Dorsal views of cranidia, both ×6. Fig. 90, It.14307. Fig. 91, It.14308.

Fig. 92 *Cyphoproetus* sp. (p. 222). Derfel Limestone, Nant Aber Derfel. It.14309. Dorsal view of cranidium, ×15.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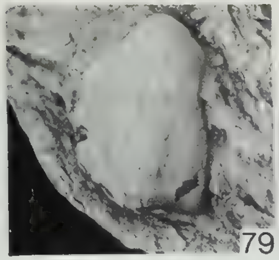
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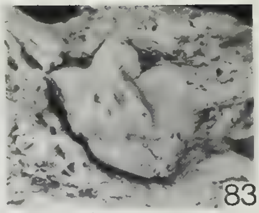
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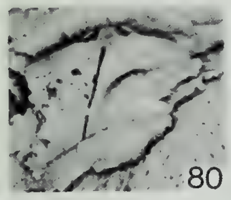
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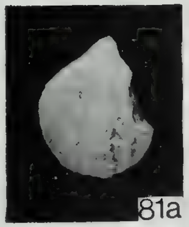
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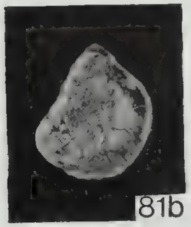
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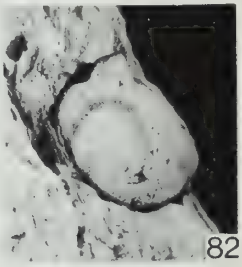
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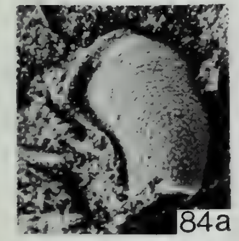
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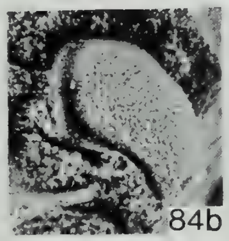
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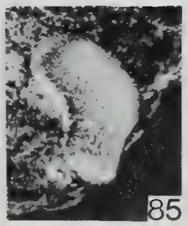
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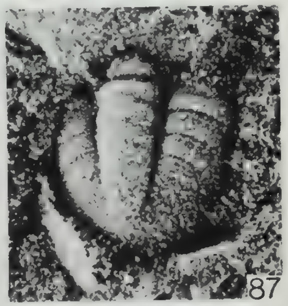
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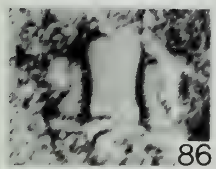
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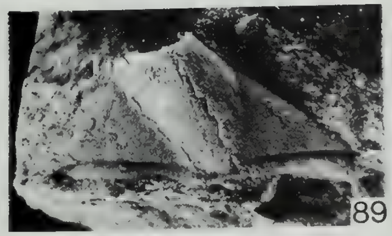
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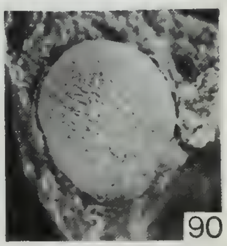
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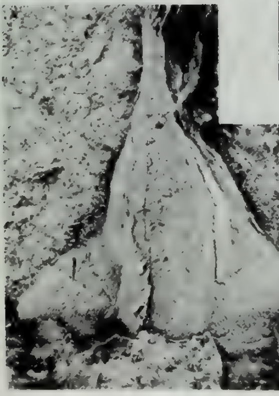
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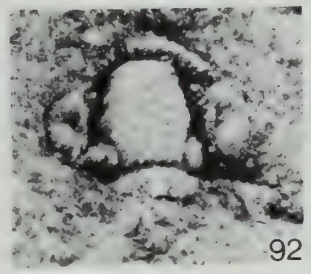
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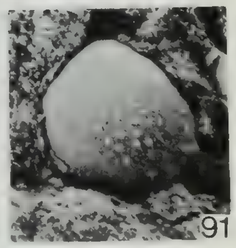
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Family **RAPHIOPHORIDAE** Angelin, 1854

Genus ***LONCHODOMAS*** Angelin, 1854

Lonchodomas sp.

Figs 88–89

MATERIAL AND LOCALITIES. Five cephalic specimens (It.14301–5) from bed R52 at Rhiw March and a single cephalic specimen (It.14306) from bed R49 are the first record of this genus in the Lower Bala Group.

Family **CHEIRURIDAE** Salter, 1864

Genus ***SPHAEROCORYPHE*** Angelin, 1854

Sphaerocoryphe sp.

Figs 90–91

MATERIAL AND LOCALITY. Two spherical, pustulose glabellae (It.14307–8) from bed R52 in the Cymerig Limestone at Rhiw March are the first record of this genus in the Lower Bala Group.

Family **PROETIDAE** Salter, 1864

Genus ***CYPHOPROETUS*** Kegel, 1927

Cyphoproetus sp.

Fig. 92

MATERIAL AND LOCALITY. The internal and external mould of a cranidium (It.14309) from the type Derfel Limestone at Nant Aber Derfel (SH 850395) is the first record of this genus in the Ordovician of Wales.

Phylum **MOLLUSCA**

Class **BIVALVIA** Linné, 1758

Introduction

Recent studies by Brenchley (1966), Pickerill (1974), Hurst & Hewitt (1977), Hurst (personal communication 1978) and Pickerill & Brenchley (1979) show that the Mollusca, and in particular the Bivalvia, are, after the Articulata (Brachiopoda) and Trilobita, one of the most important classes of organism found in the shelly facies of the Caradoc Series in Wales and the Welsh Borderland. But their importance has not been emphasized, and in Wales, largely because of poor preservation and indistinctive, mainly external morphology, the class has received little attention. Since the above authors record the occurrence and distribution of various bivalve genera in Wales and the Welsh Borderland, distinctive forms recovered from the Lower Bala Group are noted here.

Although Ordovician Bivalvia from eastern North America (Bretsky 1970, Pojeta 1971) are generally more common in contemporary Middle to Upper Ordovician deposits of the Appalachians (Bretsky, personal communication 1977), and the overall distribution of Anglo-Welsh Caradoc Bivalvia has yet to be outlined in any detail, the occurrence of congeneric taxa in both areas implies reasonable prospects for future correlations and comparisons.

Figured material

The forms figured here are assigned to genera but not described in any detail. In general the material from the Bala area is less abundant and well-preserved than that from the Berwyns and Salop. Any attempt at full systematic description of the Bala material would prove unrewarding without detailed consideration of other, more abundant material in other parts of the Anglo-Welsh region, but full locality details are given for the material discussed.

Order **NUCULOIDA** Dall, 1889

Family **PRAENUCULIDAE** McAlester, 1969

Genus ***CARDIOLARIA*** Munier-Chalmas, 1876

? ***Cardiolaria*** sp.

Figs 93–95

MATERIAL AND LOCALITIES. Internal moulds of nuculoid bivalves from beds AD A (PL 4441–3) and loc. 35 (PL 4440) in the middle part of the Allt Ddu Formation are provisionally assigned to ? *Cardiolaria* sp. The four numbered specimens have respective height and length measurements (mm) as follows: 2·5 and 4·0; – and 3·5; 3·0 and 5·0; 3·5 and 5·5 (means 3·0 and 4·5). Dentition is observed in the first two specimens.

Family **MALLETIIDAE** Adams & Adams, 1858

Genus ***NUCULITES*** Conrad, 1841

Nuculites sp.

Fig. 96

MATERIAL AND LOCALITY. A single phosphatized internal mould of an articulated specimen (PL 4444), height 5·0 mm, length 8·0 mm, was recovered by Mr P. Magor from the locally-developed limestone beds in the lower part of the Nod Glas at Pistyll Gwyn. The posterior part of the hinge exhibits about 12 poorly-preserved, fine teeth each about 0·2 mm in width.

DISCUSSION. The above two nuculoids, though uncommon in most of the succession, are the only sessile benthos recovered from parts of the 'faunal depletion zone' in the middle part of the Allt Ddu Formation. They are considered to be infaunal deposit feeders. In the absence of better-preserved material Dr N. J. Morris, who has helped the author with the identification of bivalve taxa, has suggested that forms resembling the genera *Praenucula* and *Palaeosolen* are also present amongst the unfigured material collected from the middle part of the Allt Ddu Formation.

Order **MODIOMORPHOIDA** Newell, 1965

Family **MODIOMORPHIDAE** Miller, 1877

Genus ***MODIOLOPSIS*** Hall, 1847

Modiolopsis sp.

Figs 97, 98

MATERIAL, LOCALITIES AND DISCUSSION. Specimens (PL 4445 and PL 4446a, b) from beds at loc. 928 (8990 2234) and from bed AD 3J, respectively, in the upper part of the Allt Ddu Formation are assigned to the genus *Modiolopsis*. The Modiomorphidae are usually considered to have been byssally attached, semi-infaunal or epifaunal suspension feeders.

Order **ARCOIDA** Stoliczka, 1871

Family **CYRTODONTIDAE** Ulrich, 1894

Genus ***CYRTODONTA*** Billings, 1858

Cyrtodonta sp.

Figs 99–101

MATERIAL, LOCALITIES AND DISCUSSION. Specimens from beds GG 1X (PL 4447), AD 0 (PL 4448) and H13 (PL 4449) are assigned to this genus. The former, an articulated specimen, was found in presumed life position with the umbones pointing downwards. Another specimen, PL 4450 from bed CYG 5 (see Fig. 8, p. 179), is assigned to ? *Cyrtodonta* sp.

Order **PHOLADOMYOIDA** Newell, 1965
Family **GRAMMYSIIDAE** Miller, 1877
Genus *CUNEAMYA* Hall & Whitfield, 1875
Cuneamya sp.
Figs 102a–c

MATERIAL, LOCALITY AND DISCUSSION. A single, well-preserved specimen (PL 4451) of an articulated *Cuneamya* was recovered from bed AD 3H in the Allt Ddu Formation. This genus is commonly regarded as having had a burrowing, infaunal mode of life.

Discussion of the Bivalvia

Brenchley (1966), Pickerill (1974) and Pickerill & Brenchley (1979) record *Modiolopsis*, *Goniophorina*, *Arca*, *Psilonychia* and *Vlasta* in their *Howellites* Community, *Byssodesma*, *Psilonychia* and a pteriacean in the *Dinorthis* Community and *Colpomya* in the *Dalmanella* Community. Pickerill (1974) also referred to *Ambonychia*, *Ctenodonta* sp. and *M. modiolaris* in the Berwyn area. Most of the bivalves in the Caradoc Series of north and central Wales are confined to the Soudleyan Stage.

Dr J. M. Hurst has collected a large number of bivalves from the Caradoc Series of Shropshire, many of which are congeneric with, or otherwise closely related to, bivalves from Wales. The author, who is currently examining some of this material, has collected *Cyrtodonta* from the lower part of the Chatwall Flags (Soudleyan) and has also examined faunas rich in nuculoid bivalves from the Acton Scott Beds. In the light of forthcoming publications on the Shropshire faunas, however, further comment on the known and recently-discovered bivalvia is considered premature.

Class **GASTROPODA** Cuvier, 1797

Elles (1922) recorded the gastropod genera *Cyclonema*, *Bellerophon* (*Sinuites*), *Lophospira* and *Murchisonia* in the Caradoc Series at Bala. In the present study representatives of the three former genera have been recorded in 55 of the 196 samples corresponding to the main sections (Figs 2, 8, 12–15). Dr J. S. Peel confirmed the identifications and noted that two distinct species of

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Figs 93–95 ? *Cardiolaria* sp. (p. 223). Allt Ddu Formation, south side of Pen y Cefn Coch. Figs 93a, b, PL 4440. Left-lateral and anterior views of internal mould of an articulated specimen, both ×7·5. Fig. 94, PL 4442. Internal mould of a right valve, ×6. Fig. 95, PL 4443. Internal mould of a right valve, ×9.

Fig. 96 *Nuculites* sp. (p. 223). Limestone beds beneath the Cymerig Member in the Nod Glas Formation at Pistyll Gwyn, near Llanymawddwy. PL 4444. Right-lateral view of internal mould of an articulated specimen, ×5.

Figs 97–98 *Modiolopsis* sp. (p. 223). Allt Ddu Formation. Fig. 97, Craig y Gath, near Llangower. PL 4445. Right-lateral view of external mould of an articulated specimen, ×1·5. Fig. 98, north of Graig Ty nant, near Llanymawddwy. PL 4446a. External view of a right valve, ×1·5.

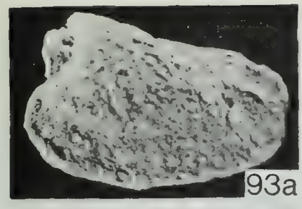
Figs 99–101 *Cyrtodonta* sp. (p. 223). Figs 99–100, Allt Ddu Formation. Fig. 99, west of Gelli-grîn Farm, Bala. PL 4448. Left-lateral view of an articulated specimen, ×2. Fig. 100, Craig y Gath, near Llangower. PL 4447. External mould of a left valve, ×4·5. Fig. 101, Llaethnant Formation, Afon Twrch, near Bwlch y Groes. PL 4449. External mould of a left valve, ×4·5.

Figs 102a–c *Cuneamya* sp. (above). Allt Ddu Formation, Craig y Gath, near Llangower. PL 4451. Dorsal, anterior and left lateral views of the external mould of an articulated specimen, all ×2.

Fig. 103 ? *Archinacella* sp. (p. 226). Nod Glas Formation, Rhiw March, Llanymawddwy. PG 5022. Left-lateral view of an internal mould of a complete specimen, ×6.

Fig. 104 *Balacrinus basalis* (M'Coy) (p. 226). Allt Ddu Formation, Rhiw March, Llanymawddwy. E 67750. External mould of cup remains and attached arm and pinnule remains, ×2.

Fig. 105 *Stenaster obtusus* (Forbes) (p. 226). Allt Ddu Formation, Ty nant Farm, south of Llanuwchllyn. E 53698. Internal mould of a complete specimen, ×4.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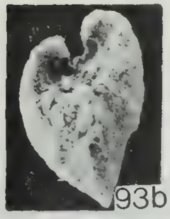
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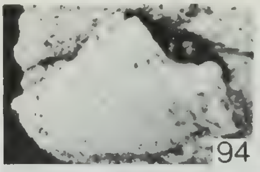
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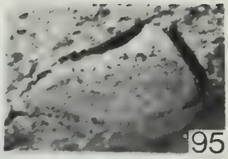
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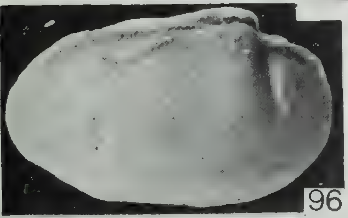
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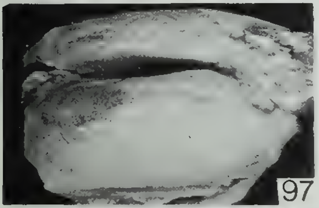
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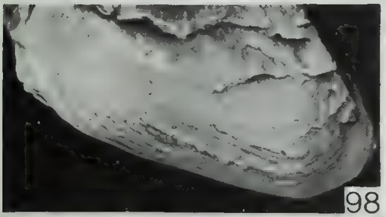
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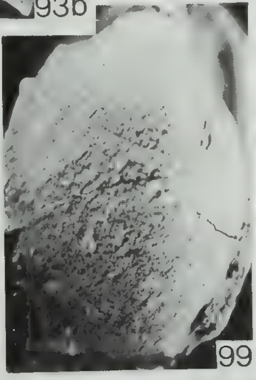
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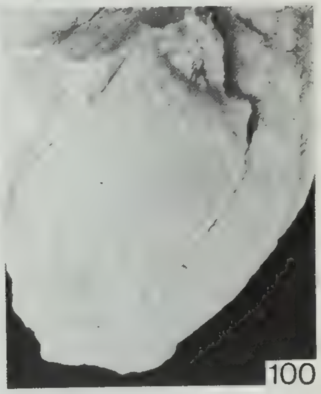
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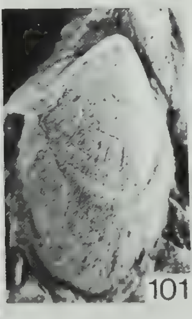
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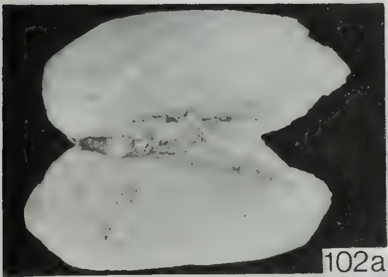
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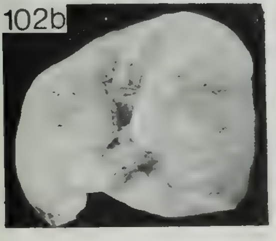
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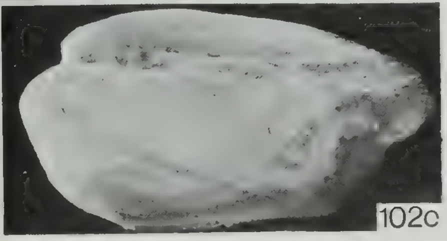
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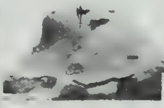
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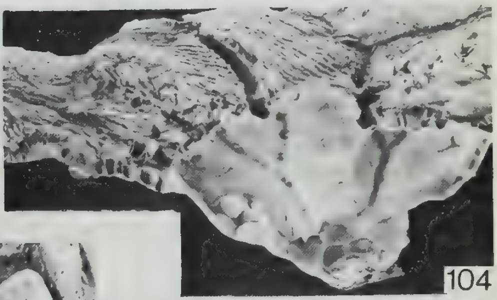
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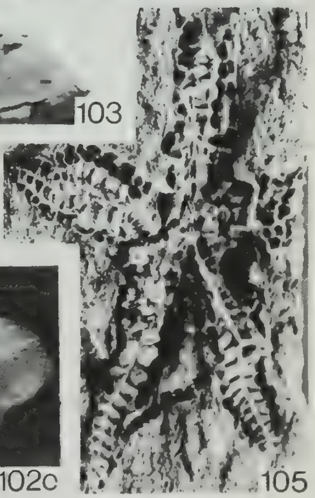
105

Cyclonema are found, in the Allt Ddu and Gelli-grîn formations respectively. Material from this study is not figured here.

Pickerill & Brenchley (1979) record *Cyclonema*, *Cyrtolites*, ? *Seelya*, *Sinuites* and *Bucanopsis* from the *Howellites* Community, and *Lophospira* and *Murchisonia* in the *Dinorthis* and *Dalmanella* Communities respectively. Pickerill (1974) also referred to *Bucania* sp. and *Kokenospira* in the Lower Cwm Rhiwarth Siltstones.

Class **MONOPLACOPHORA** Wenz *in* Knight, 1952
Family **ARCHINACELLIDAE** Knight, 1956
Genus ***ARCHINACELLA*** Ulrich & Scofield, 1897
? ***Archinacella*** sp.

Fig. 103

A single asymmetrically conical shell mould (PG 5022) from bed R45 at the base of the Nod Glas Formation resembles *Archinacella* and is provisionally assigned to this genus.

Class **CEPHALOPODA** Cuvier, 1797

MATERIAL AND DISCUSSION. Although representatives of the Cephalopoda are recorded in 33 of the 196 samples corresponding to the main sections, most material is poorly preserved. However, a single well-preserved specimen (C 81324) from bed H40 (Fig. 4, p. 176) is assigned to ? *Orthoceras* and deposited with the other material figured here.

Phylum **ECHINODERMATA**
Class **CRINOIDEA** Miller, 1821
Subclass **CAMERATA** Wachsmuth & Springer, 1885
Family **ARCHAEOCRINIDAE** Moore & Laudon, 1943
Genus ***BALACRINUS*** Ramsbottom, 1961
Balacrinus basalis (M'Coy)

Fig. 104

MATERIAL, LOCALITY AND DISCUSSION. A well-preserved external mould (E 67750) of cup showing characteristic plate pattern, arm and pinnule remains was recovered from sample R14 in the Allt Ddu Formation at Rhiw March. Despite the occurrence of numerous fragmentary crinoid remains in the majority of samples (see Figs 4, 6–9, 12–15, 17) this specimen is the only complete one recovered during this study.

Class **STELLEROIDEA** Lamarck, 1816
Subclass **OPHIUROIDEA** Gray, 1840
Order **STENURIDA** Spencer, 1951
Family **STENASTERIDAE** Schuchert, 1914
Genus ***STENASTER*** Billings, 1858
Stenaster obtusus (Forbes)

Fig. 105

MATERIAL, LOCALITY AND DISCUSSION. A complete internal mould (E 53698) was recovered from beds immediately above the Frondderw Ash in the stream at Ty Nant (SH 906262); this is the same horizon from which sample 1022B was obtained (Fig. 6A, p. 178). The specimen is from a similar stratigraphical horizon (associated with the Frondderw Ash) to the Moel y Garnedd locality from which Salter recovered a specimen (Spencer 1927 : pl. 23). Elles (1922 : 138) recorded another ophiuroid *Protaster salteri* (Salter, *ex* Forbes) from immediately above the Cefn Gwyn Ash (Cefn Gwyn) (Spencer 1934 : pl. 31).

Faunal communities and associations

Unlike the Silurian faunas categorized by Zeigler (1965), Ziegler *et al.* (1968) and others into benthic 'communities', British Ordovician faunas have not, until recently, been classified in any such way, but elsewhere, e.g. in eastern North America, several Ordovician communities have been named by Bretsky (1969) and others.

Williams (1973 : 242–243) concluded that the Lower and Middle Caradoc faunas of Wales and the Welsh Borderland contained four facies-related 'faunal associations' (or 'communities'), named after *Dinorthis*, *Nicolella*, *Onniella* and *Howellites*, which are respectively characterized by 4, 5, 2 and 1 other named brachipod genera. He also named a fifth association, the '*Bicuspina* set', which is characteristic of the Upper Llandeilo and Lower Caradoc succession of the Shelve area (Williams 1976 : 39); the quantitative composition of this set (Williams 1974 : tables 7–11) allows it to be distinguished, by cluster analysis, from two other pre-Caradoc, inarticulate-dominated Shelve sets. The *Bicuspina* set is readily compared with the *Dinorthis* Association as they contain elements in common, in particular *Dalmanella*, *Heterorthis* and *Bicuspina* itself.

Pickerill (1974, 1977 : figs 3, 4) and Pickerill & Brenchley (1979) followed Williams (1973) by naming a *Dinorthis*, a *Nicolella*, an *Onniella*, a *Howellites* and a *Dalmanella* 'community' from the South Berwyns; the *Dinorthis* community is considered to consist of component *Dinorthis* and *Macrocoelia* 'sub-communities', which are essentially analogous to 'populations' referred to by Bretsky (1970). Unlike Williams they used quantitative measurements of ubiquity and average abundance to define four of these five communities; they referred only briefly to the fifth, *Onniella* community with associated genera. As the author, independently, chose to define the associations named here in a similar fashion to the quantitative method of Pickerill & Brenchley, an excellent opportunity is afforded for comparisons between the compositions of related associations in adjacent areas. Like Williams (1973, 1976) and Pickerill & Brenchley (1979) I use dominant genera in naming the associations described here; this permits the following direct comparisons.

The *Howellites* community of the South Berwyns is essentially similar to the contemporary *Howellites–Paracraniops* Association described here; both occur in a mudstone or silty mudstone facies and have *Howellites*, *Paracraniops*, *Macrocoelia*, *Reuschella*, *Bicuspina*, *Leptaena*, *Sowerbyella*, *Broeggerolithus* and *Brongniartella* amongst the more persistent (ubiquitous) and abundant elements. The main difference between the two associations is the relative importance of *Sowerbyella* in the South Berwyns. This is partly a reflection of a difference in the range of strata considered in the two areas; if the fauna of pre-middle Allt Ddu beds bearing *Sowerbyella* and *Heterorthis* were considered in conjunction with the upper Allt Ddu association the compositional resemblance of the associations in these two areas would be even more striking.

The composition of the *Howellites–Kloucekia* Association (and the closely related marginal *Howellites* association, Fig. 19, p. 193) is quite distinct, in detail, from the other *Howellites*-dominated associations referred to here. The brachiopods *Paracraniops*, *Macrocoelia*, *Reuschella*, *Bicuspina*, *Leptaena* and *Sowerbyella* and the trilobite *Brongniartella* are rare, absent or, like *Howellites* and *Broeggerolithus*, represented in this association by species distinct from those found in the older association(s) elsewhere. The association is further characterized by the relative persistence of *Skenidioides* and *Kloucekia*.

Although *Howellites* and *Broeggerolithus* are characteristic of all associations incorporating the name *Howellites*, it is clear that the Allt Ddu and Gelli-grîn associations of the area south of Bala are quite distinct and should not be considered jointly as Williams (1973) has done.

The *Dinorthis* Association, *sensu* Williams, although recognized by Pickerill & Brenchley in the South Berwyns, has not been identified in the Lower Bala Group south of Llanuwchllyn. Current evidence suggests that it is recognizable in parts of the Soudleyan succession in the Bala area (*sensu* Bassett *et al.* 1966) but not in equivalent beds to the south. For example, *Dinorthis* is a dominant element in sample GG1X (Fig. 12, p. 184) but is rare in equivalent beds at Craig y Gath (Fig. 8, p. 179) and unknown in the equivalent Rhiw March section (Fig. 9, p. 180). Williams (1973) states that the association is characterized by *Bicuspina*, *Dalmanella*, *Heterorthis* and *Leptaena;* this is confirmed by Pickerill & Brenchley (1979) who recognize these genera together with *Howellites*, *Reuschella*, *Sowerbyella*, *Paracraniops*, *Macrocoelia*, *Broeggerolithus* and *Brongniartella* amongst the dominant and persistent elements of the *Dinorthis* sub-community in the South Berwyns. It is significant that these latter seven genera are all of equivalent importance in the South Berwyn *Howellites* community and the *Howellites–Paracraniops* Association. However, in the *Dinorthis* sub-community (*sensu* Pickerill & Brenchley 1979) of south Salop, *Bicuspina* and *Reuschella* are not recorded whereas *Harknessella* and *Salopia* are considered important elements. At various specified horizons in the Salop, south Berwyns, Breidden Hills and Snowdonia successions, these authors consider the community to be represented by the *Macrocoelia* sub-community which, apart from being dominated by this genus, is essentially similar in composition to the *Dinorthis* sub-community. Similarly, their *Dalmanella* community, which is not recognized in the Bala area, is composed essentially of elements which characterize their *Howellites* and *Dinorthis* communities; its only very distinctive feature is the relative importance of *Dalmanella*.

The *Kullervo–Nicolella–Palaeostrophomena* Association (Williams *in* Whittington & Williams 1955), the *Nicolella* association/community *sensu* Williams (1973) and of Pickerill & Brenchley (1979) and the phases of the *Nicolella–Onniella* Association (defined here) are clearly closely related. The six brachiopod genera, including *Nicolella*, referred to by Williams as components of the association are not those which are most characteristic of the Welsh associations. Pickerill & Brenchley (1979) and the present study have shown, for their respective associations, that the most dominant and persistent elements are *Nicolella*, *Dolerorthis*, *Skenidioides*, *Eoplectodonta*, *Leptestiina*, *Onniella*, *Platystrophia*, *Bicuspina* and *Reuschella*. Of these *Platystrophia* is particularly abundant in the South Berwyns, but not at Bala, whilst *Onniella*, *Eoplectodonta*, *Reuschella* and *Bicuspina* are considerably more important in this latter area.

In the area considered here the importance of *Onniella* and *Eoplectodonta* in the *Nicolella–Onniella* Association cannot be overlooked. Not only are both forms considerably more abundant, at certain horizons, than any other brachiopod genera but they also represent a 'dalmanellid–plectambonitacean combination' noted in numerous Ordovician faunal associations in Britain and elsewhere. The so-called *Onniella* association/community referred to by Williams/Pickerill & Brenchley, although not quantitatively defined, appears to differ from the *Onniella* associations of this paper.

The *Onniella–Sericoidea* Association quantitatively outlined here is clearly related to the *Onniella* association/community referred to by Williams/Pickerill & Brenchley. Both the Pen y Garnedd Shale and Dyfi Mudstone associations contain *Onniella*, *Sericoidea* and *Paterula*. This particular dalmanellid–plectambonitacean association is typical of argillaceous parts of the Caradoc Series elsewhere in Britain. For example, Hurst (personal communication 1978) reports an *Onniella–Sericoidea* type of association in the Onny Shales. Similarly, Dean (1959) described Marshbrookian to Pusgillian faunas characterized by *Onniella* and *Chonetoidea* (and *Sericoidea*, A. D. Wright, personal communication 1975) from the Cross Fell area.

The *Sericoidea* Association of the Pistyll Gwyn, Y Ceunant and Aber Cowarch sections (Figs 17 & 19, pp. 190–193) is simply a diluted (low diversity, low equitability) marginal variety of the *Onniella–Sericoidea* Association. Between Bala and Dinas Mawddwy there is a pronounced lateral variation in the faunal associations (and facies) of the uppermost 20 m of the Caradoc succession. The *Nicolella–Onniella* Association (occupying coarse, calcareous clastic substrates) passes laterally into the *Onniella–Sericoidea* and *Sericoidea* Associations (calcareous mudstones), then into a graptolitic association (in black shales); see Fig. 18, p. 192.

Contemporary Scoto-Irish faunas described by Williams *et al.* (1962) and Mitchell (1977) have yet to be categorized into named associations. These faunas are fundamentally different from those of 'Anglo-Welsh' affinity; this is a reflection of the mid-Ordovician separation of northern and southern Britain by the Proto-Atlantic ocean (Smith *et al.* 1973). The discovery of *Bimuria* and *Protozyga* in Wales and the recognition of wider distributions for *Cyclospira*, *Palaeostrophomena* and *Anisopleurella* are evidence of more mixing of Scoto-Irish with Anglo-Welsh faunas than was hitherto supposed.

Despite the fact that Whittington & Williams (1955 : 398) and Williams (1962 : table 2; 1969 : 131–135) have shown that faunal associations with Scoto-American (or Scoto-Appalachian) affinities show little similarities to those known from the Anglo-Welsh region, recent studies by Bayer (1967), Fox (1968), Bretsky (1969, 1970), Bretsky & Bretsky (1975, 1976), Walker & Laporte (1970), Walker (1972), Walker & Alberstadt (1975), Walker & Parker (1976) and others have led to the naming of a number of associations or communities from the Mid- to Upper Ordovician of the Appalachians which show striking parallels with those named from the Anglo-Welsh region.

Among these 'American communities' are several named after familiar dalmanellid–plectambonitacean combinations including the *Onniella–Sowerbyella* community (Bretsky 1969), the *Eoplectodonta* (*Thaerodonta*)–*Onniella* community (Bayer 1967) of the mid-continent upper Ordovician and the *Resserella–Sowerbyella* assemblage (Fox 1968); similarly, data given by Titus & Cameron (1976 : 1216–1217) reveal that *Paucicrura* and *Sowerbyella* represent about two-thirds (mean relative abundance) of the total fauna in four out of five communities named after rarer elements.

Other communities named after or dominated by genera common to the Anglo-Welsh successions are as follows. The mid-Appalachian *Rafinesquina*, *Sowerbyella*, *Lophospira* Association and the *Onniella*–nuculoid bivalve Association named by Bretsky (1969) from siltstones and mudstones respectively, as component associations (or 'populations') in the *Sowerbyella–Onniella* community, are reminiscent of parts of the Berwyn and Salopian faunal successions respectively. Similarly, the succession dominated by *Onniella* and *Cryptolithus* outlined by Bretsky & Bretsky (1975 : 228) from the upper Ordovician of Quebec is shown subsequently by these authors (1976 : table 3) to be dominated at different horizons by combinations of genera including *Nuculites* with *Cryptolithus* and *Nuculites* with *Onniella* (cf. Bretsky 1969). Such combinations are again reminiscent of parts of the Anglo-Welsh Caradoc successions.

The upper Ordovician *Platystrophia–Leptaena* assemblage (Fox 1968) is comparable to the *Nicolella* community (*sensu* Pickerill & Brenchley 1979) which, in addition to occurring in a similar calcareous facies, contains these two former genera amongst its most important elements.

Walker & Laporte (1970) and Walker (1972) referred to *Strophomena* and *Dalmanella* respectively as 'major' taxa in inferred low intertidal and subtidal carbonate facies of the middle Ordovician of New York. Similarly, Walker & Alberstadt (1975) and Walker & Parker (1976) have named a *Rostricellula–Strophomena* community from the middle Ordovician of the southern Appalachians. All these genera represent important or dominant elements in parts of broadly contemporary Anglo-Welsh successions.

Although Williams (1969 : 133–137) referred to *Sowerbyella*, *Sericoidea*, *Macrocoelia*, *Rafinesquina*, *Strophomena*, *Platystrophia*, *Dalmanella*, *Howellites* and *Onniella* as widespread or pandemic genera in Caradoc to Ashgill times, there has hitherto been little comment on their importance as 'community dominants' in parts of both the American and north European provinces. In the Anglo-Welsh and Appalachian regions the importance of dalmanellid–plectambonitacean dominated associations cannot be overemphasized; combinations like *Dalmanella* with *Sowerbyella* (in the Upper Llanvirn–Llandeilo of south Wales) and the other Caradoc to Ashgill combinations mentioned above occupy a wide variety of facies including limestones, tuffs, sandstones, siltstones and fine mudstones.

Conclusions

The present study suggests that detailed local examination of (Caradoc) faunal successions can lead to the identification of distinct associations dominated by different species of the same, often ubiquitous, genera. Since associations are commonly named after such dominant forms, a paradoxical situation arises, where on the one hand local interassociation variation is easily demonstrated, yet on the wider provincial scale considerable uniformity appears to be the rule. Such a paradox is the result of a dual influence. Firstly, the use of generic rather than specific terminology in the naming of communities, although favouring brevity, masks important differences. Secondly, the widespread occurrence of various species of ubiquitous genera strongly suggests that 'parallel communities' (*sensu* Thorson 1957, 1966) characterized Ordovician marine benthic environments. For these reasons it is emphasized that the generic names employed in the classification of associations should refer unequivocally to particular species at particular horizons, as stated or implied here in all cases. This approach permits named communities to be specifically identified and distinguished from other local or distant, more or less contemporary parallel communities dominated by ubiquitous congeneric forms.

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References

Addison, R. 1974. *The biostratigraphy of the Llandeilo Facies of South Wales.* Ph.D. Thesis, Univ. of Belfast (unpubl.).

Anderson, F. W. 1964. The law of ostracod growth. *Palaeontology*, London, **7**: 85–105.

Antia, D. D. J. 1977. A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England. *Paleobiol.*, Menlo Park, **3** : 404–414.

Bancroft, B. B. 1945. The brachiopod zonal indicies of the Stages Costonian–Onnian in Britain. *J. Paleont.*, Menasha, **19** : 181–252, pls 22–38.

Bassett, D. A., Whittington, H. B. & Williams, A. 1966. The stratigraphy of the Bala district, Merionethshire. *Q. Jl geol. Soc. Lond.*, **122** : 219–271.

Bayer, T. N. 1967. Repetitive benthonic community in the Maquoketa Formation (Ordovician) of Minnesota. *J. Paleont.*, Tulsa, **41** : 417–422.

Brenchley, P. J. 1966. *The Caradoc rocks of the north and west Berwyns.* Ph.D. Thesis, Univ. of Liverpool (unpubl.).

Bretsky, P. W. 1969. Central Appalachian Late Ordovician communities. *Bull. geol. Soc. Am.*, Boulder, Col., **80** : 193–212.

—— 1970. Upper Ordovician ecology of the Central Appalachians. *Bull. Peabody Mus. nat. Hist.*, New Haven, **34** : 1–150.

—— **& Bretsky, S. S.** 1975. Succession and repetition of Late Ordovician fossil assemblages from the Nicolet River Valley, Quebec. *Paleobiol.*, Menlo Park, **1** : 225–237.

—— —— 1976. The maintenance of evolutionary equilibrium in late Ordovician benthic marine invertebrate faunas. *Lethaia*, Oslo, **9** : 223–233.

Bruton, D. L. 1976. The trilobite genus *Phillipsinella* from the Ordovician of Scandinavia and Great Britain. *Palaeontology*, London, **19** : 699–718.

Calef, C. E. & Hancock, N. J. 1974. Wenlock and Ludlow marine communities. *Palaeontology*, London, **17** : 779–810.

Cocks, L. R. M. 1978. A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's Monograph. *Palaeontogr. Soc.* (*Monogr.*), London. 256 pp.

Cooper, G. A. 1956. Chazyan and related brachiopods. *Smithson. misc. Collns*, Washington, **127** : 1–1024, 1025–1245, pls 1–269.

Cisne, J. L. 1973. Life history of an Ordovician trilobite *Triarthrus eatoni*. *Ecology*, *Brooklyn*, **54**: 135–142.

Davidson, T. 1869. A Monograph of the British Fossil Brachiopoda. Part VII. The Silurian Brachiopoda. **3**: 169–248, pls 23–37. *Palaeontogr. Soc.* (*Monogr.*), London.

Dean, W. T. 1959. The stratigraphy of the Caradoc Series in the Cross Fell Inlier. *Proc. Yorks. geol. Soc.*, Hull, **32** : 185–228.

Elles, G. L. 1922. The Bala country: its structure and rock succession. *Q. Jl geol. Soc. Lond.*, **78** : 132–175.

Fox, W. T. 1968. Quantitative palaeoecologic analysis of fossil communities from the Richmond Group. *J. Geol.*, Chicago, **76**: 613–641.

Fürsich, F. T. 1977. Corallian (upper Jurassic) marine benthic associations from England and Normandy. *Palaeontology*, London, **20** : 337–385.

Harrington, H. J. *et al.* 1959. Arthropoda I. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology* **O**. xix + 560 pp., 415 figs. Lawrence, Kans.

Hancock, N. J., Hurst, J. M. & Fürsich, F. T. 1974. The depths inhabited by Silurian brachiopod communities. *J. geol. Soc. Lond.*, **130** : 151–156.

Hunt, A. S. 1967. Growth variation and instar development of an agnostid trilobite. *J. Paleont.*, Tulsa, **41** : 203–208.

Hurst, J. M. 1975. Some observations on the brachiopods and the level-bottom community ecology of Gotland. *Geol. För. Stockh. Förh.*, **97** : 250–264.

—— 1979. The stratigraphy and brachiopods of the upper part of the type Caradoc of South Salop. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **32** (4): 183–304.

—— **& Hewitt, R. H.** 1977. On tubular Problematica from the type Caradoc (Ordovician) of England. *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **153** : 2, 147–169.

Krebs, C. J. 1978. *Ecology. The experimental analysis of distribution and abundance.* (2nd edn.) London, 694 pp.

Lockley, M. G. 1977. *The geology of the Llanuwchllyn to Llanymawddwy area*, . . . (&c.). Ph.D. Thesis, Univ. of Birmingham (unpubl.).

—— 1978. The application of ecological theory to palaeoecological studies with particular reference to equilibrium theory and the Ordovician system. *Lethaia*, Oslo, **11** : 281–291.

—— 1980. The geology of the Llanuwchllyn to Llanymawddwy area, south Gwynedd, North Wales. 21 msp, 9 figs. *Geol. J.*, Liverpool, **15** (1) (In press.)

—— **& Williams, A.** (1980). Lower Ordovician Brachiopoda from mid and south-west Wales. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **34** (4) (In press.)

MacArthur, R. H. 1965. Patterns of species diversity. *Biol. Rev.*, Cambridge, **40** : 510–533.

MacGregor, A. R. 1961. Upper Llandeilo brachiopods from the Berwyn Hills, north Wales. *Palaeontology*, London, **4** : 177–209.

Margalef, R. 1958. Information theory in ecology. *Gen. Systs*, Ann Arbor, Mich., **3** : 36–71.

Mitchell, W. I. 1977. The Ordovician Brachiopoda from Pomeroy, Co. Tyrone. *Palaeontogr. Soc.* (*Monogr.*), London. 138 pp., 28 pls.

Murray, J. W. & Wright, C. A. 1974. Palaeogene Foraminiferida and Palaeoecology, Hampshire and Paris Basins and the English Channel. *Spec. Pap. Palaeont.*, London, **10** : 1–129.

Neyman, A. A. 1967. Limits to the application of the trophic group concept in benthic studies. *Oceanology*, Washington, **7** : 149–155 [transl. from Russian of *Okeanologiya*, Moscow, **7** (2) : 195–202].

Palmer, A. R. 1957. Ontogenetic development of two Ollenellid trilobites. *J. Paleont.*, Tulsa, **31** : 105–128.

Petersen, C. G. J. 1924. A brief survey of the animal communities in Danish waters . . . . *Am. J. Sci.*, New Haven, (5) **7** : 343–354.

Pickerill, P. K. 1974. *Geology of the south Berwyn Hills* (*North Wales*) . . . (&c.). Ph.D. Thesis, Univ. of Liverpool (unpubl.).

—— 1977. Trace fossils from the upper Ordovician (Caradoc) of the Berwyn Hills, central Wales. *Geol. J.*, Liverpool, **12** : 1–16.

—— **& Brenchley, P. J.** 1979. Caradoc marine benthic communities of the south Berwyn Hills, north Wales. *Palaeontology*, London, **22** : 229–264.

Pielou, E. C. 1969. *An Introduction to Mathematical Ecology*. 286 pp. London.

Pojeta, J., jr 1971. Review of Ordovician Pelecypods. *Prof. Pap. U.S. geol. Surv.*, Washington, **695**. 46 pp., 20 pls.

Pugh, W. J. 1923. The geology of the district around Corris and Aberllefenni. *Q. Jl geol. Soc. Lond.*, **79** : 50–51.

—— 1928. The geology of the district around Dinas Mawddwy (Merioneth). *Q. Jl geol. Soc. Lond.*, **84** : 345–381.

—— 1929. The geology of the district between Llanymawddwy and Llanuwchllyn (Merioneth). *Q. Jl geol. Soc. Lond.*, **85** : 242–306.

Raw, F. 1927. The ontogenetics of trilobites, and their significance. *Am. J. Sci.*, New Haven, (5) **14** : 7–35, 131–149, 240; 25 figs.

Rogers, M. J. 1976. An evaluation of an index of affinity for comparing assemblages, in particular of Foraminifera. *Palaeontology*, London, **19** : 503–515.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.*, Lancaster, Pa., **102** : 243–282.

—— 1969. Benthic marine diversity and the stability-time hypothesis (contrib. 2353, Woods Hole Oceanogr. Inst.). *In* Diversity and stability in ecological systems. *Brookhaven Symp. Biol.*, Upton, N.Y., **22** : 71–81.

Scott, R. W. 1974. Bay and shoreface benthic communities in the Lower Cretaceous. *Lethaia*, Oslo, **7** : 315–330.

Sedgwick, A. & M'Coy, F. 1851–55. *A synopsis of the classification of the British Palaeozoic Rocks, with a systematic description of the British Palaeozoic Fossils* . . . (&c.) xcviii + 661 pp., 27 pls. London & Cambridge.

Smith, A. G., Briden, J. C. & Drewry, G. E. 1973. Phanerozoic world maps. *In* Hughes, N. F. (ed.), Organisms and continents through time. *Spec. Pap. Palaeont.*, London, **12** : 1–42.

Spencer, M. A. 1913–65. British Palaeozoic Asterozoa. Parts I–X, with supplement and index by H. G. Owen. *Palaeontogr. Soc.* (*Monogr.*), London. 583 pp., 37 pls.

Thorson, G. 1957. Bottom communities (sublittoral or shallow shelf). *In* Hedgpeth, J. W. (ed.), Treatise on marine ecology and paleoecology, 1. *Mem. geol. Soc. Am.*, Washington, **67** (1) : 461–534.

—— 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.*, Den Helder, **3** : 267–293.

Titus, R. & Cameron, B. 1976. Fossil communities in the Lower Trenton Group (Middle Ordovician) of central and northwestern New York State. *J. Paleont.*, Tulsa, **50** : 1209–1225.

Turpaeva, E. T. 1948. [The feeding of some benthic invertebrates of the Barents Sea.] *Zool. Zh.*, Moscow, **27** (6) : 503–512. (In Russian.)

Valentine, J. W., 1972. Conceptual models of ecosystem evolution. *In* Schopf, T. J. M. (ed.), *Models in Paleobiology* : 192–215. San Francisco.

—— 1973. *Evolutionary paleoecology of the marine biosphere*. 511 pp. New Jersey.

Walker, K. R. 1972. Community ecology of the Middle Ordovician Black River Group of New York State. *Bull. geol. Soc. Am.*, Boulder, Col., **83** : 2499–2524.

—— **& Alberstadt, L. P.** 1975. Ecological succession as an aspect of structure in fossil communities. *Paleobiol.*, Menlo Park, **1** : 238–257.

—— **& Laporte, L. F.** 1970. Congruent fossil communities from the Ordovician and Devonian of New York. *J. Paleont.*, Tulsa, **44** : 928–944.

—— **& Parker, W. C.** 1976. Population structure of a pioneer and a late stage species in an Ordovician ecological succession. *Paleobiol.*, Menlo Park, **2** : 191–201.

Watkins, R. M. 1975. *British Ludlow palaeoecology and its bearing on the Silurian marine ecosystem*. D.Phil. Thesis, Univ. of Oxford (unpubl.).

—— 1979. Benthic community organization in the Ludlow Series of the Welsh Borderland. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **31** (3) : 175–280.

Whittington, H. B. 1962-68. The Ordovician tribolites of the Bala area, Merioneth. Parts I-IV. *Palaeontogr. Soc.* (*Monogr.*), London. 138 pp., 32 pls.

—— **& Williams, A.** 1955. The fauna of the Derfel Limestone of the Arenig district, North Wales. *Phil. Trans. R. Soc.*, London, B **238** : 397–427.

Williams, A. 1962. The Barr and Lower Ardmillan Series (Caradoc) of the Girvan district, south-west Ayrshire, with decriptions of the Brachiopoda. *Mem. geol. Soc. Lond.*, **3** : 1–267.

—— 1963. The Caradocian brachiopod faunas of the Bala district, Merionethshire. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **8** : 327–471.

—— 1969. Ordovician faunal provinces with reference to brachiopod distribution. *In* Wood, A. (ed.), *The Pre-Cambrian and Lower Palaeozoic rocks of Wales* : 117–154. Cardiff.

—— 1973. Distribution of brachiopod assemblages in relation to Ordovician palaeogeography. *In* Hughes, N. F. (ed.), Organisms and continents through time. *Spec. Pap. Palaeont.*, London, **12** : 241–269.

—— 1974. Ordovician Brachiopoda from the Shelve district, Shropshire. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) Suppl. **11** : 1–163, pls 1–28.

—— 1976. Plate tectonics and biofacies evolution as factors in Ordovician correlation. *In* Bassett, M. G. (ed.), *The Ordovician System* : 29–66. Cardiff (Proc. palaeont. Ass. Symp., Birmingham 1974).

—— ***et al.*** 1972. A correlation of Ordovician rocks in the British Isles. *Spec. Rep. geol. Soc. Lond.*, **3** : 1–74.

Wright, A. D. 1970. The stratigraphic distribution of the inarticulate brachiopod *Orthisocrania divaricata* (M'Coy) in the British Isles. *Geol. Mag.*, Cambridge, **107** (2): 97–103.

Ziegler, A. M. 1965. Silurian marine communities and their environmental significance. *Nature, Lond.*, **207** : 270–272.

——, **Cocks, L. R. M. & Bambach, R. K.** 1968. The composition and structure of Lower Silurian marine communities. *Lethaia*, Oslo, **1** : 1–27.

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Synopsis

The palaeontology, sedimentology and stratigraphy of the Insect Bed (Bembridge Marls) are discussed and previous work summarized. Five insect orders are revised, notes on the biology of living relatives are included and the palaeoecology considered. Isoptera: *Mastotermes anglicus* von Rosen is redescribed, *Sisyra* (?) *disrupta* Cockerell is transferred from the Neuroptera to *Kalotermes* s. lat. (Kalotermitidae); a species of *Reticulitermes* (Rhinotermitidae) and a termitid are described but not named. The Isoptera suggest a warm subtropical–tropical climate. Plecoptera: *Nemoura priscula* Cockerell is transferred to the genus *Leuctra* (Leuctridae). Megaloptera: the record of *Raphidia* is shown to be erroneous. Neuroptera: Mantispidae: *Mantispa relicta* Cockerell is transferred to *Promantispa* gen. nov. Hemerobiidae: *Hemerobius tinctus* sp. nov., ? *Neuronema* spp. A and B, and 3 unnamed species are described. Chrysopidae: a species of Chrysopinae (s. lat.) is described but not named. The affinities of an extinct sisyrid are discussed. Mecoptera: *Panorpa veterna* Cockerell (Panorpidae) is transferred to the genus *Bittacus* (Bittacidae); an unnamed species of *Bittacus* is described. Lepidoptera: *Micropterix anglica* sp. nov.

(Micropterigidae), *Paratriaxomasia solentensis* gen. et sp. nov. (Tineidae), *Copromorpha fossilis* sp. nov. (Copromorphidae), *Pyralites preecei* sp. nov. (Pyralidae), *Nymphalites zeuneri* sp. nov. (Nymphalidae), *Prohepialus* sp. (Hepialidae) and *Geometridites larentiiformis* sp. nov. (Geometridae) are described. *Lithopsyche antiqua* Butler is transferred to the Lycaenidae and the placement of *Gurnetia durranti* Cockerell in the Cossidae is questioned. A tineid, a tentative gelechioid, 12 other species of microlepidoptera and a possible papilionoid are described but not named.

Introduction

The Bembridge Marls are a predominantly argillaceous formation, 21–36 m thick, preserved only in the northerly half of the Isle of Wight in southern England (Fig. 1). Near the base of the formation is a thin clay bed, generally less than a metre thick, with concretions and tabular bands of fine-grained argillaceous limestone and hard marl. The latter, on the NW coast near Cowes, have been noted for their insect remains for just over a century and constitute the 'Insect Limestone' of authors (Daley 1973*a*). However, the calcareous and argillaceous developments together form a distinct unit (*ibid.*) and the name Insect Bed (Bembridge Marls) used by Curry (1958) for a single limestone is here applied collectively. This horizon has yielded the only sizeable insect fauna in the British Tertiaries above the Lower Eocene, some fifteen orders being represented. The fauna also includes molluscs, an ostracod, an anostracous crustacean, an isopod, arachnids (spiders) and avian remains (feathers, Fig. 61, p. 268), the last three of which are scarce. Although named after the insects, the bed is probably better known in the palaeontological literature for its flora due to the work of Reid & Chandler (1926). However, apart from the leaves of a reed, well-preserved plant macrofossils are rare. Insect fragments are fairly frequent, and richer pockets are sometimes encountered (Jarzembowski 1976). The most extensive collections from this bed are now preserved in the British Museum (Natural History). These were largely collected by E. J. A'Court Smith (1814–1900), collecting between West Cowes and the Newtown River from about 1859 (Smith 1874). Apparently he discovered the insects following a comment by Forbes (1856 : 58–59) on the insect-bearing nature of some similar limestones in the Purbeck Beds (late Jurassic–early Cretaceous) on the mainland (Hughes 1922 : 67; Jackson 1933). Much of A'Court Smith's material subsequently went to R. W. Hooley and the Rev. P. B. Brodie, and the history of the collections and their acquisition by the Museum are given in Reid & Chandler (1926) and Crane & Getty (1975). Notable smaller collections from the Insect Bed include one at the Museum of Isle of Wight Geology, which was mainly the work of G. W. Colenutt, and another consisting of some of Brodie's material in the Lacoe Collection at the United States National Museum; I have myself collected from the bed since 1966.

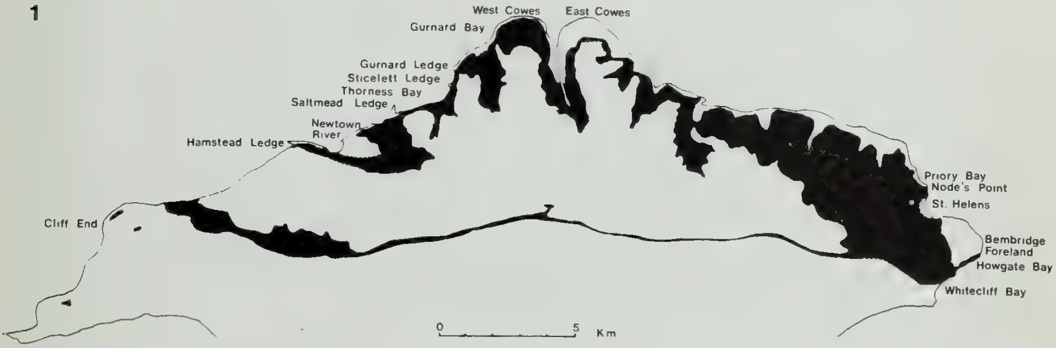


Fig. 1 Outcrop map of the Bembridge Marls.

The fossil insect collections at the British Museum (Natural History) contain over 3900 pieces of 'Insect Limestone' of which a large proportion bear two or more specimens. However, a number of these are indeterminate and some species, especially in the Formicidae, are represented by numerous examples. The present paper is confined to the Isoptera, Plecoptera, Neuroptera, Mecoptera and Lepidoptera, which although rare or uncommon have yielded a varied range of taxa; several other orders are being studied. All available material is documented, and in addition to systematic and taxonomic considerations, the ecological and biological requirements of Recent relatives are briefly discussed.

Previous studies

A'Court Smith (1874) appears to be the first published record of the occurrence of arthropod remains in the Insect Bed near Cowes. Woodward (1878, 1879) published a list of identifications made by Frederick Smith of the Department of Zoology, British Museum (Natural History), based on a sample of A'Court Smith's collection. In the 1879 paper Woodward described an anostracan, *Branchipodites vectensis*, and an isopod, *Eosphaeroma fluviatile*, from the same horizon; Martini (1972) showed the latter to be a synonym of the continental species *Eosphaeroma margarum* (Desmarest 1822). McCook (1888*a*, *b*) gave two identical descriptions of a mygalomorph spider, *Eoatypus woodwardii*, and Jones & Sherborn (1889) described an ostracod *Potamocypris brodiei* which Haskins (1968) compared with *Cypridopsis*, another freshwater genus.

The first description of an insect, *Lithopsyche antiqua* Butler 1889, was accompanied by a colour plate. This was followed by von Rosen (1913) on fossil *Mastotermes*, and in 1915, T. D. A. Cockerell described 33 new insect species from the Lacoe Collection. He subsequently made selective studies of the main collection at the BM(NH): Cockerell (1917*a*, 1921*a*, *b*, *c*, 1922); Cockerell & Andrews (1916); Cockerell & Haines (1921). The Formicidae were studied by Donisthorpe (1920), the Culicidae by Edwards (1923) and Orthoptera by Zeuner (1939). These constitute the main works on the insect fauna and, although the flora was monographed by Reid & Chandler (1926), there is no comprehensive work on the arthropods. Chandler (1964) reviewed the Bembridge Flora, including the microfloral work of Machin (née Pallot) published later in 1971. Although the junction of the Bembridge Marls and Bembridge Limestone is unconformable (Daley & Edwards 1971), the palaeobotanists considered the Bembridge Beds to contain a single flora, and it is not always clear which taxa occur in the Insect Bed. Daley (1969) studied the palaeoenvironment of the Bembridge Marls, and (1971, 1972*a*) was specifically concerned with sedimentary deformational structures in the 'Insect Limestone'. Jarzembowski (1976) first recorded insects in this bed on the east side of the island near St Helens, 18 km from Cowes.

Notes on lithology, inclusions and method of study

The insect-bearing lithology is usually a fine-grained argillaceous limestone with a conchoidal fracture and blue-grey colouration when fresh. It weathers externally producing a distinctive brownish yellow rind, and on broken surfaces the weathered zone has a sharp junction with the unweathered material. Older pebbles, especially near West Cowes, may only have a small region of 'blue' near the centre, and the weathered zone occasionally shows concentric colour banding. At outcrop it occurs in dark blue-grey clay as oval concretions, up to 20 cm thick, or as thinner tabular bands, and can be of a more marly constitution; thin, laterally continuous shell bands delimit the bed (Figs 2–4, p. 242). The calcareous developments tend to occur in courses within the clay more or less parallel to the bedding, which is of local stratigraphic value. There is a definite arching of the upper shell bed over large concretions, but in some places the undulations are less easy to explain.

Silty laminae, 1–4 mm thick and 3–90 mm apart, are usually evident in the limestone, marked by finely-comminuted carbonaceous detritus. They appear to have no vertical regularity and erosional bases are occasionally evident. The laminae may contain ostracod valves, fragments of drifted vegetation the only common recognizable ones being of *Typha latissima* Braun – and insect wings and body fragments; groups of shells belonging to the freshwater genus *Galba* sometimes occur. The freshwater genera *Hippeutis* and *Viviparus* also occur but are infrequent. Plant fossils are usually accompanied by a brown carbonaceous residue, and small black fragments of vegetable material are occasionally present. One of the latter has been examined and identified as natural fusain by Professor T. M. Harris. The limestone has yielded some small grains of resin: one of these (In.17436) was analysed by infrared spectroscopy, but the spectra obtained were too weak for comparison with those of other Tertiary resins.

The laminae occasionally yield concentrates of articulated insect bodies, often associated with abundant, complete examples of *Branchipodites vectensis*, but such rich developments appear to be very local. Salt pseudomorphs, comminuted shell débris, seeds, spiders and portions of bird feathers are rare: the last are the only vertebrate fossils found. Insect bodies and wings are normally preserved in good relief, although substantial compression is evident in some of the more argillaceous laminae; well-preserved insects as well as fragments occur in the interbedded limestone, but there is never any concentration of material. Chitin is absent only from weakly sclerotized areas and the colour pattern may be well preserved: comparison with related forms in the living fauna indicates that some colours are close to those in life (pp. 259, 262). The body cavities are often infilled with a pink calcareous material which obscures structures, but external moulds in the enclosing matrix show very fine detail (Fig. 59, p. 267) and the 'Insect Limestone' has been justifiably referred to as 'opaque amber'.

The insects are predominantly imagines of small to medium size. The preservation of relief and soft-bodied, immature stages (Fig. 62, p. 268) as well as the fragile *Branchipus*-like crustacean, together with the arching of the upper shell bed, indicate early lithification of the matrix, but the occasional penetration of burrows from above, and development of the small-scale sedimentary deformation described by Daley (1971, 1972*a*) and evident in the limestone at all the main localities, suggest that it was not immediate. Pantin (1958) provides evidence for the length of time involved in the formation of diagenetic calcareous concretions. It is likely that the limestone was formed within several thousand years of deposition of the sediment, and perhaps less judged by the preservation of the soft-bodied arthropods. I have not observed any insect macrofossils in the clays adjacent to fossiliferous concretions although a similar lamination is evident on fresh surfaces.

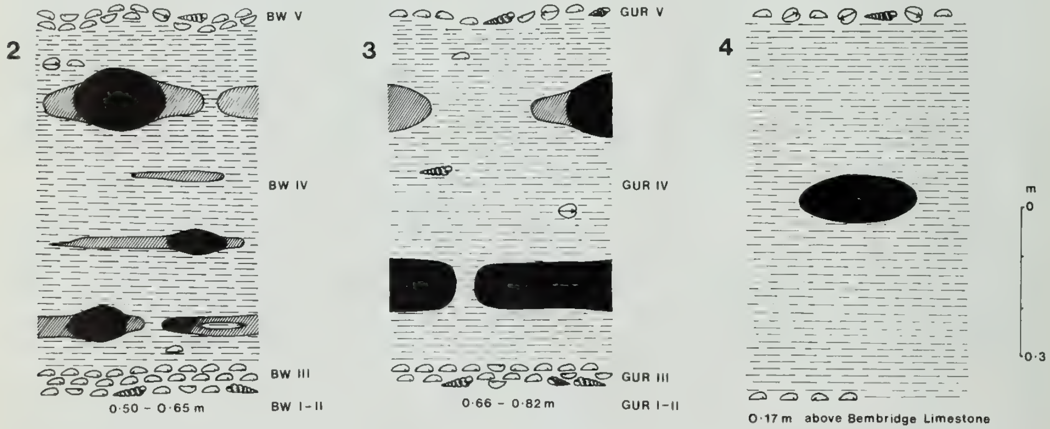
The remarks so far are based on the north-western localities. Whilst the lithological comments apply equally well on the east coast, there are some differences in the biota. St Helens and Priory Bay have yielded five orders of insects but only a few more complete specimens and the occasional ostracod and plant fragment. The author has only collected here since late 1975 and it is likely that more will be found. However, sustained search near Bembridge Foreland has yielded only a single insect specimen (see p. 243). Whilst the calcareous part of the Insect Bed is well developed and can be traced south into Whitecliff Bay, no fossils were found except for two fragments of lymnaean shell near the middle of Howgate Bay. The fossiliferous localities for insects are therefore confined to the northern part of the outcrop area of the Bembridge Marls (Fig. 1). Insect remains do occur at other levels in the formation, but very few specimens have been found to date. The A'Court Smith collection includes examples in a clay-ironstone matrix from the north-west coast, and I have seen one or two fragments in the sideritic ironstone concretions from the upper part of the Bembridge Marls littering the shore near Whitecliff Bay Point (Daley 1973*b*).

Where the limestone is exposed in the lower part of a cliff or slump and is accessible to marine erosion, it is usually well represented amongst the blocks and pebbles of the upper part of the shore, and splitting of this débris can be more rewarding. A hand-lens is necessary for examining fractured surfaces and small forms are more readily observed in oblique light. Specimens are rarely exposed properly owing to the curved fracture of the rock and both halves may show unique features. All the necessary preparation for this study was done by the author under a microscope with an electric engraver (vibrotool) or a tungsten needle. Routine examination of rock specimens under the microscope (× 16) also revealed a number of forms previously unnoticed. The examination of chitinous material was often facilitated by immersing the specimen in liquid to heighten contrast; as the matrix may contain salt, especially the softer limestone and hard marl, aqueous solutions were avoided and xylene was used for short examinations and paraffin for longer periods. Dry examination was also aided by using oblique lighting from several directions and referring to modern specimens of related forms.

Field sections

Natural exposures of the Insect Bed are confined to coastal sections and there appear to be no inland records from artificial excavations. The sections were examined between summer 1976 and spring 1977.

North-west coast. The 'Insect Limestone' is developed here only to the east of the Newtown River (Fig. 1, p. 239). The Insect Bed is represented by a thin band of clay just west of the river behind Hamstead Ledge and appears to be absent at Cliff End (Daley 1973*a*). Across the river, the strata descend gently on the eastern limb of the Porchfield anticline and the bed is seen at 433927[1], a short distance before the western end of Saltmead Ledge. It is exposed in the lower part of the cliff for some 500 m as far east as 438928 and fossiliferous blocks occur on the shore. The bed is 0·65–0·85 m thick and four calcareous courses are recognizable (Fig. 2). The uppermost includes some large concretions and may account for the thinness of the course below. At 440930 two blocks of limestone were seen apparently *in situ* in the upper part of the foreshore. Pebbles of 'Insect Limestone' die out on the beach a short distance east of Saltmead Ledge (=Thorness Point/Ledge).



Figs 2–4 Sections of the basal part of the Bembridge Marls. Fig. 2, near Saltmead Ledge. Fig. 3, immediately south of Gurnard Ledge. Fig. 4, near St Helens. (Black: limestone. Oblique shading: hard marl. Dashed lines: laminated marly clay. Bivalve: Corbiculidae. Small gastropod: *Tarebia*. Large gastropod: *Potamides*. The bed numbers to the right of Figs 2–3 are after Daley 1973*a*).

The bed is next seen on the east side of Thorness (=Thorney) Bay, where a limestone course outcrops on the upper part of the foreshore behind Sticelett Ledge (461941). The bed gradually rises from the shore north towards Gurnard Ledge (=Gurnard Point) on the northern limb of the Thorness syncline and is about 2 m above cliff base behind the latter (463946). It is best exposed in the low cliff for some 140 m south of the ledge and is 0·65–0·75 m thick. Two calcareous courses are developed: a lower more or less continuous tabular band of limestone (Insect Bed of Curry 1958) and an upper discontinuous band of concretions, often less well cemented (Fig. 3). The clay yields sporadic examples of worn *Potamides* and corbiculid valves, rare examples of the latter also being found in the calcareous part. Between Gurnard Ledge and Gurnard (=Gurnet) Bay there is a kilometre of tumbled cliff line in the Bembridge Beds but there are no further sections in the Insect Bed on the northern coast of the island before St Helens. Some characteristic limestone was however found at several points amongst the slips 500–800 m NE of Gurnard Ledge, rising towards Gurnard from approximately 6 to 11 m above cliff base. Pieces of fossiliferous limestone occur amongst the shore débris as far as West Cowes (490966).

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[1] National Grid Reference, 100 km square 40 (SZ), as are the subsequent references.

A'Court Smith worked along the coast from West Cowes to the Newtown River (White 1921) although the specimens are generally labelled 'Gurnet (or Gurnard) Bay'. The most important collecting site was on the east side of Thorness Bay where the limestone outcropped on the shore (Brodie 1878, Reid 1889), which suggests that it was at Sticelett Ledge, and the latter has recently produced some relatively well-preserved material (Jarzembowski 1976). G. W. Colenutt refers to the site as Sticelett in correspondence (*ibid.*) but an accompanying sketch map by the same author is less helpful.

East Coast. Commencing in the north, a section of the Insect Bed is found NE of St Helen's Church (Fig. 4), 200–300 m south of Node's Point (638900). Although numerous blocks of limestone occur in the SW corner of the adjacent Priory Bay, no sections were observed amongst the slips. At the Point the bed is 9 m above the base of the cliff, and 0·7 m at the southern end of the section as the strata dip towards the axis of the Bembridge syncline. It is 0·60–0·85 m thick with a single course of limestone concretions. The lower shell bed is only well-developed in the southern part of the section.

Continuing south, the Insect Bed is next seen near Bembridge Foreland, 2·7 km SE of St Helens, where a limestone course outcrops on the upper part of the foreshore amongst the beach cover and can be traced into Howgate Bay. At 654872 the limestone is 15 cm thick and yielded a single *Oecophylla* wing. Further south the bed is seen in the lower part of the cliff near Whitecliff Bay Point, gradually ascending to the cliff top in Whitecliff Bay: the limestone becomes replaced by a more marly course, and there are no insect remains.

Correlation

Edwards (1966) gives a summary of the stratigraphy of the younger Palaeogene strata of the Hampshire Basin and an extensive bibliography is found in Edwards (1971). The Bembridge Marls are near to the Eocene–Oligocene boundary, but different workers have drawn it variously above and below the formation. Edwards (1966) followed Curry (1958) who regarded the Bembridge Marls as of Oligocene, Lattorfian age, but as can be seen from Table 1, there is still no general agreement on the position of the boundary. The Insect Bed (Bembridge Marls) can therefore be considered as of late Eocene or early Oligocene age, with an absolute dating of about 35 million years BP (cf. Cavelier & Pomerol 1977).

Table 1 The age of the Bembridge Marls according to various authors, 1966–76

Oligocene : Lattorfian	Edwards 1966
Oligocene : Lattorfian	Curry 1966
Middle Oligocene : early Rupelian	Rey 1967
Lower Oligocene	Castel 1968
Eocene : Ludian	Cavelier 1968
Oligocene : Tongrian	Denizot 1968
Upper Eocene or Lower Oligocene	Curry, Gulinck & Pomerol 1969
Oligocene : Lattorfian	Daley 1969
Oligocene : Tongrian	Haskins 1971
Late Eocene–early Oligocene	Keen 1972
Lower Oligocene	Martini 1972
Late Eocene or early Oligocene	Bosma & Schmidt-Kittler 1972
Late Eocene or early Oligocene	Bosma 1974
Early Oligocene	Stinton 1975
Upper Eocene : late Priabonian	Cavelier & Pomerol 1976

Systematic descriptions

The family and higher classification follows the papers of Gay, Riek and Common (all 1970) with the following departures: the Leuctrinae are regarded as a family following modern usage, a superfamily classification of the Neuroptera is not adopted because of lack of general agreement, and the classification of the Lepidoptera is also based on Karsholt & Nielsen (1976).

Cockerell (1917*b* : 12) mentioned that he had described a species of *Raphidia* (order Megaloptera) from the Insect Bed; in fact (1917*a* : 373) he actually described a species of *Riphidia* (order Diptera : Tipulidae) which is a mis-spelling of *Rhipidia* Meigen 1818.

A supplementary list of the material examined in the course of this study is deposited in the Palaeontology Library of the British Museum (Natural History). Except where otherwise indicated, the material is from the Insect Bed (Bembridge Marls) on the NW coast of the Isle of Wight, between West Cowes and the Newtown River. The figures prefixed 'I.' or 'In.' are registration numbers of the Department of Palaeontology, British Museum (Natural History) (BM(NH)) and the material is currently housed in the Department of Entomology at the same institution. The major collections are abbreviated thus:

S :	E. J. A'Court Smith
H :	R. W. Hooley
B :	P. B. Brodie
MIWG :	Museum of Isle of Wight Geology

Other collections are named in full.

Wing veins are referred to by standard abbreviations; damaged or faint veins or margins are indicated by dashed lines, folds by dashed-and-dotted lines and extrapolations by dotted lines.

Order ISOPTERA
Family MASTOTERMITIDAE

Genus *MASTOTERMES* Froggatt, 1896

TYPE SPECIES. *Mastotermes darwiniensis* Froggatt 1896 by monotypy; Recent, Australia.

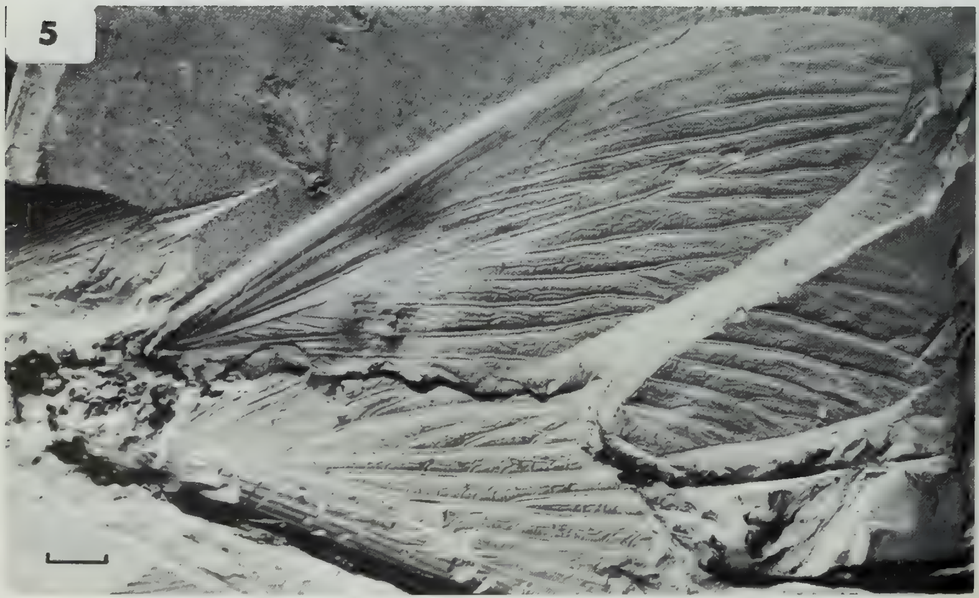
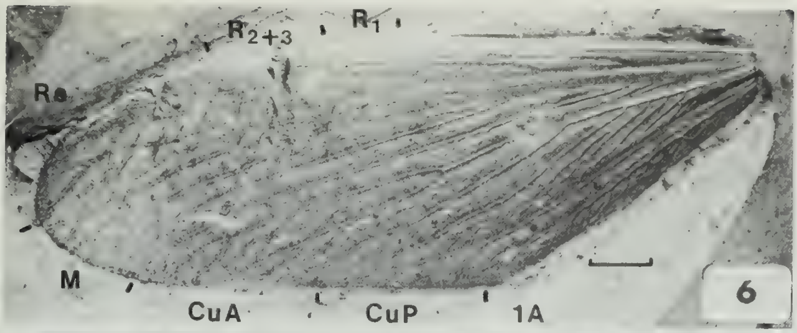
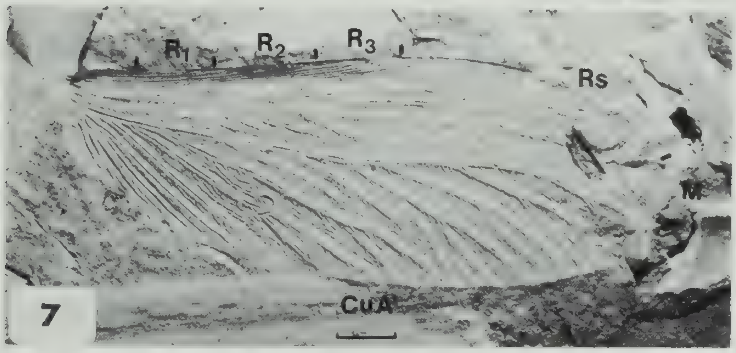


Fig. 5 *Mastotermes anglicus* von Rosen. In.24571. (Scale line = 2 mm)





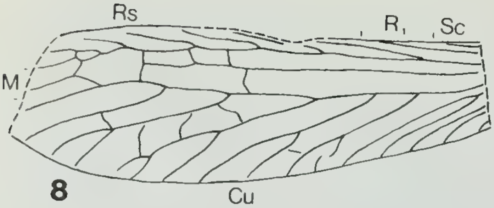
Figs 6–7 *Mastotermes anglicus* von Rosen. Fig. 6, **lectotype** (hindwing), I.15037. Fig. 7, paralectotype (forewing, I.15033. (Scale line = 2 mm)

Mastotermes anglicus von Rosen
Figs 5–7, 15, 20

1879 *Phryganea* F. Smith *in* Woodward : 344.
1913 *Mastotermes anglicus* von Rosen : 322; pl. 27, figs 5–8.
1965 = *Mastotermes batheri* von Rosen 1913; Emerson : 29.

EMENDED DESCRIPTION. *Forewing:* elongate, some incomplete specimens suggesting that a greater elongation is possible than in the specimen figured by von Rosen (1913 : pl. 27, fig. 7). Sc short and single. R_1 forking distad or basad of humeral suture, the outer branch terminating on the anterior margin at 0·2–0·4 of the forewing length (as measured from the suture). R_2 and R_3 elongate and separate at suture, R_2 sometimes forked. Stem of Rs terminating near wing apex with a more or less marked anterior curve in its distal part. Rs with about four branches to the anterior margin, the outer ones usually subdivided. M and Cu separate at suture, the former closer to Rs than CuA with one to three major branches distally and perhaps several short branches towards base. In the left forewing of In.17143 and right forewing of I.8659, M is briefly linked with Rs near base. Rs and CuA are closer in some specimens than in von Rosen's figure with M nearly median. CuA occupies about half of the wing area, dividing some ten times, the branches frequently forking once and occasionally several times. Humeral suture arcuate with maximum apical extension near M, and the basal part of the forewing is usually downcurved anterior to Rs. A brown pigmentation is often preserved on the scale, parts of M and on the more anterior veins. Forewings are preserved in 24 specimens and probably in two others.

Hindwing: elongate, rounded apically; anterior and posterior margins nearly parallel, apex nearer the latter. Sc single, elongate, on average about five times as long as in the forewing; some faint branches to the anterior margin may be present. R_1 long terminating at 0·6 of the wing length from base, with none to four subparallel branches. R_{2+3} has a common stem with Rs and



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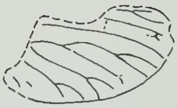

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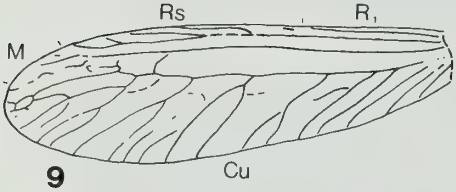

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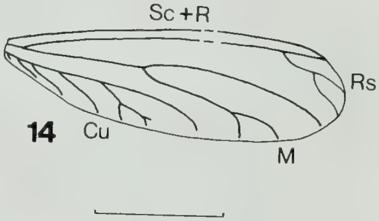

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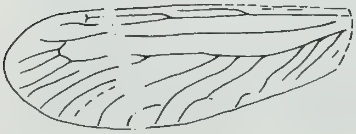

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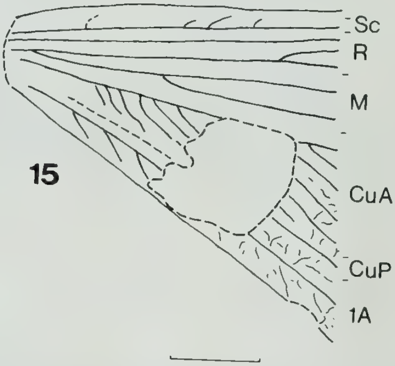

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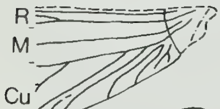

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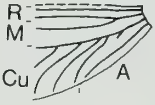

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Figs 8–13 *Kalotermes disruptus* (Cockerell) comb. nov. Fig. 8, In.64534 (forewing). See also Fig. 17. Fig. 9, In.24619 (? hindwing). Fig. 10, In.24591 + In.24600 (hindwing). Fig. 11a, I.9845 (right forewing base). Fig. 11b, I.9845 (left forewing, anterior part of scale). Fig. 12, I.9576 (hindwing base). Fig. 13, I.8644 (holotype). See also Fig. 19.

Fig. 14 Termitidae species A, In.24603. See also Fig. 35.

Fig. 15 *Mastotermes anglicus* von Rosen, In.24610 (hindwing base).

(Scale line = 2 mm. Figs 8–14 same scale, minor reticulation and membranous irregularities omitted).

the appearance of being the first branch of the latter. Stem of Rs more or less oblique towards apex with two to four unforked major branches to the anterior margin. Stem of M nearer Rs than CuA, united with Rs at base, and producing two to three major branches to the apical part of the posterior margin. Some very short branches are developed towards the base of M. CuA dividing ten to eleven times, the branches becoming progressively shorter towards base. CuP single with a broad terminal fork. 1A parallel to anal fold with numerous short branches directed obliquely towards the latter. Anal lobe unknown, probably because it is folded under or broken away. The stem of M and the more anterior veins may show traces of brown pigmentation. As in the forewing, there is a well-developed reticulation. In addition to the lectotype, the hindwings are seen in six specimens and probably in two others.

Body: about 15 mm long and all parts pigmented brown as in Recent *Mastotermes*. Head with a well-defined Y-shaped suture. Antennae about 5·0 mm long, segments transversely oval near base, circular near middle and elongate distally. Pronotum widest anteriorly with sides strongly downcurved (Fig. 20, p. 249). In.17357 has a longitudinal groove on the underside of the abdomen near the lateral margins as in Recent *Mastotermes*. In the same specimen, sternite 7 is not enlarged, indicating that it is a male. Body remains are preserved in 17 specimens.

LECTOTYPE. I.15037 (S), designated herein. Fig. 6.

OTHER MATERIAL. There are 18 paralectotypes and 42 other specimens (including one from St Helens), plus three possible specimens.

DIMENSIONS. Lectotype: wing length (apex–approximate position of 'suture') 25·8 mm, width 8·8 mm.

Other material. *Forewing:* length from humeral suture to apex (single specimen) 20·8 mm, maximum width 7·8–8·8 mm, length of Sc 1·0–2·8 mm, maximum length of scale 2·8–3·2 mm. *Hindwing:* length from wing base to apex 27·2–29·1 mm, maximum width 8·5–8·8 mm. *Body:* head, length 3·2–4·0 mm, maximum width 2·8–3·2 mm; pronotum, length 1·9–2·0 mm, maximum width 2·8–3·8 mm.

REMARKS. Emerson (1965 : 30) states that he examined the 'holotype' and 'paratypes' of *M. anglicus* and that the species was described from three specimens. Examination of the fossil insect collection at the BM(NH) showed that three specimens of this species, labelled 'holotype' (I.15037) and 'paratype' (I.15033 and I.8989), had been singled out and in addition there were a further 18 specimens each labelled 'paratype'. Von Rosen (1913 : 321) stated that he had examined 21 specimens of *M. anglicus*, and the former three correspond to the figures of his pl. 27; a footnote (1913 : 335) says that these are 'nach den Typen', but no holotype is designated in the paper. In a reprint from von Rosen in the library of the Department of Palaeontology, BM(NH), the registration numbers of the 21 specimens are hand written in the margin; I.15037 is indicated as 'type' and the remainder as 'paratypes'. Von Rosen's material is therefore a syntypic series and I.15037 is here designated as lectotype. However, only 18 paralectotypes are recognized, as there are two pairs of part and counterpart; a further 42 specimens from the Insect Bed are also referred to this species. Eight specimens from the A'Court Smith collection, purchased in 1883 (I.15034–6, I.15038–42) are labelled 'Phryganea', with or without a roman numeral in the same unidentified hand. Woodward (1879) recorded eight specimens of the trichopterous genus *Phryganea* in the A'Court Smith collection, on the basis of which a predator and prey association with *Branchipodites vectensis* was inferred by Tasch (1969). This misidentification was, however, realized not long afterwards, for on I.8804 Brodie had written 'Phryganea' which he then crossed out and replaced by 'termite'; the specimen was purchased in 1898, a year after his death. The lectotype, a single hindwing, is adequately figured by von Rosen (1913 : pl. 27, fig. 8) except that Sc probably continues apically for twice the figured length but is intertwined with the fine anterior branches from R_1.

Both the wing and body remains indicate that *M. anglicus* is close to the living *M. darwiniensis*. The wing venation of modern primitive termites is prone to individual variation and this was also true of *anglicus*. Emerson (1965) was probably aware of the difficulty of separating the two species when he stated '*Mastotermes anglicus* seems to have a greater proportional distance between the costal border and the radial sector than does *M. darwiniensis*' (1965 : 30). The distance from the stem of Rs to the anterior margin divided by the wing width, measured near the mid-point of the wing, gave values of 0·14–0·18 and 0·15–0·18 for the fore- and hindwings respectively of the fossil species. This compares very well with the living species (cf. Gay 1970 : fig. 15.2; von Rosen 1913 : pl. 26, figs 1–2; Tillyard 1931 : pl. 21, figs 1–2). *M. anglicus* appears to differ from *M. darwiniensis* in that more branches of CuA originate directly from the main stem in the forewing: in the latter there are five–six main branches. The soldier caste is generally more useful for separating species in modern termites but only the reproductives are so far known from the Isle of Wight.

Present day *Mastotermes* is naturally confined to tropical northern Australia, although it has been introduced to New Guinea, its southern limit being the Tropic of Capricorn. The termite avoids high-rainfall areas and is absent from rainforest and areas where such forest has been cleared. It is very destructive of timber, although some trees including *Ficus* spp. are hardly affected; this genus is known from the Insect Bed (Reid & Chandler 1926; personal examination of matrix). The termite normally nests in or under the boles of trees, or in logs or stumps, and produces galleries in the soil. Alates are released in early November and have been recorded through the summer monsoon season (Gay & Calaby 1970 : 395–396).

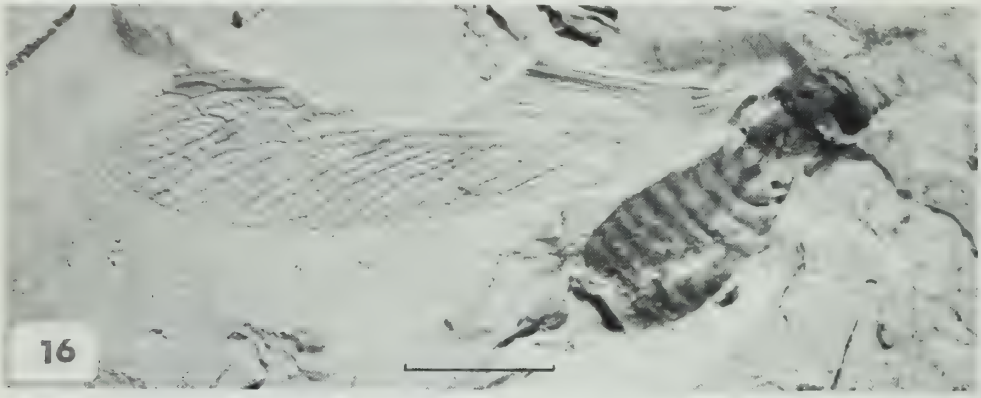


Fig. 16 *Kalotermes disruptus* (Cockerell) comb. nov. I.9845. (Scale line = 2 mm)

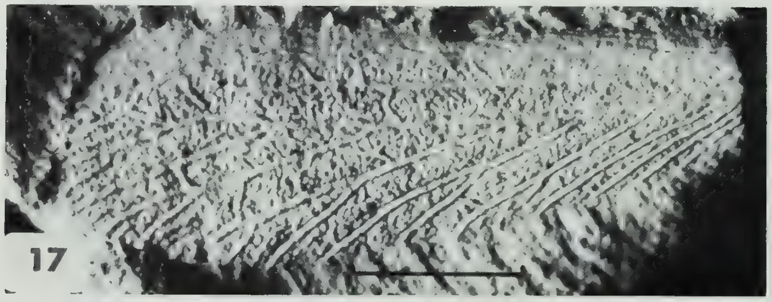
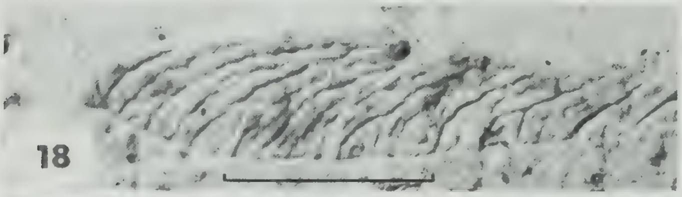


Fig. 17 *Kalotermes disruptus* (Cockerell) comb. nov. In.64534, forewing. See also Fig. 8. (Scale line = 2 mm)



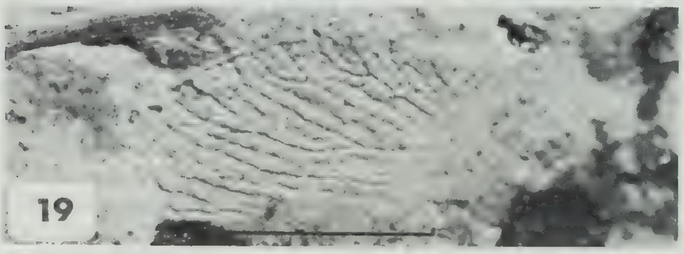
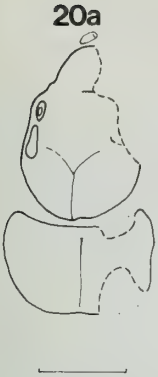
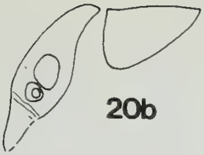
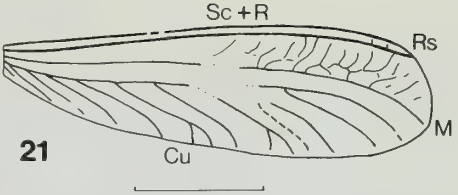


Fig. 18 In.64535, incomplete counterpart of a termite wing from the Insect Bed to show preservational similarity to Fig. 19.

Fig. 19 *Kalotermes disruptus* (Cockerell) comb. nov. Holotype, posterior margin uppermost. See also Fig. 13. (Scale line = 2 mm)







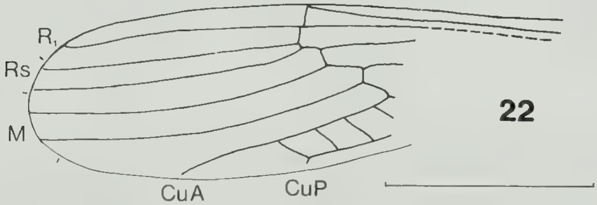


Fig. 20 *Mastotermes anglicus* von Rosen, In.43415, head and pronotum. Fig. 20a, dorsal view. Fig. 20b, lateral view.

Fig. 21 *Reticulitermes* sp., In.64535 (forewing). Venation and main reticulation only. See also Fig. 26.

Fig. 22 *Leuctra priscula* (Cockerell) comb. nov. Forewing venation. Holotype, In.17498.

(Scale line = 2 mm)

Family **KALOTERMITIDAE**

Genus ***KALOTERMES*** Hagen, 1853

TYPE SPECIES. *Termes flavicolle* Fabricius 1793, by subsequent designation; Recent, western Palaearctic.

Kalotermes disruptus (Cockerell) comb. nov.

Figs 8–13, 16–19

1917*a* *Sisyra* (?) *disrupta* Cockerell : 381; pl. 31, fig. 13.

EMENDED DESCRIPTION. The holotype consists of an apical fragment of a wing with parts of Cu, M and possibly Rs preserved. The following account is based on a series of specimens considered to be conspecific with the type.

The body is known from a single dorsal impression (I.9845). The head is missing except for traces of the basal region which indicate that it was inclined downwards at burial. Pronotum gently tapered anteriorly and with sides slightly curved ventrally; meso- and metanota subequal. Abdomen with nine visible segments, the ninth curved anteroposteriorly with blunt posterior angle. A single leg is preserved: tibia with remains of an inner terminal spur; tarsus with elongate distal segment and short basal segments.

Wings elongate, gradually widening towards the apex with maximum width at 0·3 of the length from the latter; apex rounded. R_1 single and close to the anterior margin. Costal area (stem of Rs to anterior margin) moderately wide and frequently downcurved especially near base as in Recent termites, and consequently difficult to examine. Rs with 3–6 oblique, single branches to the anterior margin. Cu occupies just over half of the wing area, branching 8–10 times. Branches of Cu running obliquely to the posterior margin and less inclined than those of Rs : they may fork once or occasionally twice at a variable distance from base. M nearly parallel to the stems of Rs and Cu, and slightly closer to the former. M may have a longish apical fork or two to three short terminal branches and may unite with Rs for a short distance apically. The terminations of Rs, M and Cu are often difficult to identify in the variable pattern of short veins or reticulations near the wing apex.

The wing membrane is finely tuberculate (in dorsal aspect) posterior to Rs; the sculpture may be well-defined (Fig. 17), or only a general irregularity of the surface may be discernible. A few crossvein-like reticulations are also developed. R_1, much of Rs and the basal portions of M and Cu often show traces of a dark brown pigmentation apparently corresponding to the more sclerotized areas in life; body light brown.

Fore- and hindwings are not readily identifiable from incomplete specimens but the former are represented by I.9845 and In.64534, and the latter by I.9576, In.24591 + In.24600 and In.24621. The humeral suture in the forewing is gently curved towards base posterior to R_1; the forewing scale has a strongly curved anterior margin and overlaps the base of the hindwing scale (I.9845). The hindwing suture is shorter and more arcuate, Rs and M separate distad of the suture, A present.

HOLOTYPE. I.8644 (B). Figs 13, 19.

OTHER MATERIAL. 14 specimens and possibly one other.

DIMENSIONS. *Wings:* length (distance from humeral suture–apex) *c.* 6·0–8·1 mm, maximum width 2·0–2·4 mm.

Body (I.9845 only): length of thorax 2 mm, length of pronotum 0·7 mm, maximum width of pronotum 1·3 mm, maximum width of meso- and metathorax 1 mm; length of abdomen 2·6 mm; length of tibia 0·6 mm.

REMARKS. Cockerell described this species from a single wing fragment, and on the basis of a comparison with Recent *Sisyra vicaria* (Walker) it was placed in the Neuroptera (Hemerobiidae: Sisyrinae). He was, however, doubtful about its generic placement (Cockerell 1917*a* : 381–382).

Comparison of the fragment with *S. vicaria* and Recent *Sisyra* spp., and with fossil insects from the Insect Bed in the BM(NH), indicates that the species should be transferred to the Isoptera, because

i. The vein pattern does not agree with Sisyridae (cf. Parfin & Gurney 1956);

ii. Neither veins nor wing margin show any trace of macrotrichia or trichosors which are present in sisyrids (*ibid.*); preservational failure is improbable when compared with other Insect Bed Neuroptera;

iii. The veins are relatively thick and lacking in pigmentation, unlike the Insect Bed Neuroptera;

iv. *S. vicaria* and the Insect Bed Neuroptera may show a faint, linear fold in the membrane between two veins, but this is different from the membranous irregularities in Cockerell's specimen;

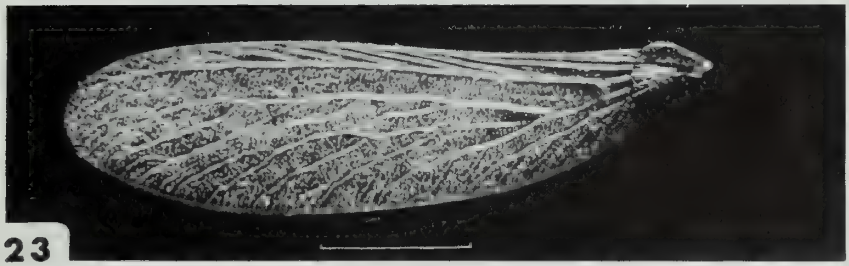
v. The fragment compares best with the negative impressions of wings belonging to a hitherto unrecognized termite in which the venation is well developed near the apex.

The type and new material are referred to the family Kalotermitidae because the pronotum is flatly arched and not narrower than the head, the anterior wing scale overlaps the hindwing scale, Sc is short and sclerotized in the forewing and absent in the hindwing, R_1 is sclerotized and single, Rs is sclerotized and parallel to the anterior margin with a number of branches to the latter, Cu is unsclerotized with numerous branches to the posterior margin and an anal vein is present in the hindwing only (Krishna 1961 : 315).

The wing sculpture is similar to Recent *Glyptotermes* Froggatt, *Rugitermes* Holmgren and *Kalotermes*, and of these three, the venation comes closest to *Kalotermes* (Krishna 1961). However, the relatively small number of branches of Rs in the forewing (Fig. 8) is more like Recent *Incisitermes* Krishna than *Kalotermes* (Krishna 1961 : 334, 354). Krishna erected the former genus for a segregate of *Kalotermes* in which one of the diagnostic characters is the absence of tuberculation of the wing membrane. Emerson (1969 : 43, 49) accepted the new genus but rejected the distinction with regards to wing sculpture. Examination of the alates of *K. flavicollis* (Fabricius), *K. rufinotum* Hill, *I. minor* (Hagen) and *I. tabogae* (Snyder) suggests to me that sculpture does not always allow a definite separation of the two genera (Figs 23–24). In *Kalotermes rhenanus* Hagen from the Oligocene of Rott, Germany, Rs has 5–8 branches in the forewing and 3–4 in the hindwing

(Emerson 1969 : 34), which compares well with the Bembridge Marls species (Figs 8–10). However, there appears to be no indication of wing sculpture in *K. rhenanus*. The costal area of the forewing is too poorly known in *disruptus* for detailed comparison with the Recent genera. Emerson (1969 : 29) expresses some uncertainty about distinguishing alates of the two genera in fossils where the dentition is unknown, and the Bembridge Marls species is therefore referred to *Kalotermes* in the wider sense.

The wings of kalotermitids are especially subject to variation (cf. Fuller 1919 : pl. 8, pl. 9 figs 124–134), and no two examples in *Kalotermes disruptus* (Cockerell) comb. nov. are likely to be exactly similar in the finer details of venation and reticulation. Recent kalotermitids are xylophagous, predominantly dry-wood termites, digestion being made possible by an abundant intestinal fauna of flagellate Protozoa. *Incisitermes* and *Kalotermes* are both hardwood termites, the former occurring in the New World and across the western Pacific and the latter with a cosmopolitan distribution (Emerson 1969 : 45; fig. 11). *Incisitermes* is warm temperate (subtropical)–tropical, but *Kalotermes* is mainly temperate (*ibid* : 45, 49), although preferring the warmer part of that zone (*ibid* : fig. 7). The Kalotermitidae are represented in Europe at the present time by a single species restricted to southern parts (Harris 1970 : 297).



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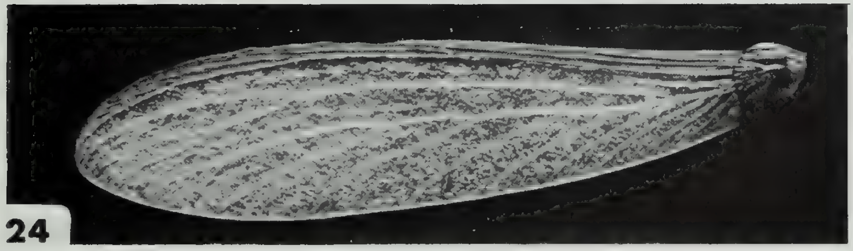

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Fig. 23 *Kalotermes flavicollis*. Recent; forewing. Oblique top lighting.

Fig. 24 *Incisitermes tabogae*. Recent; forewing. Oblique top lighting, same scale as Fig. 23. (Scale line = 2 mm)

Family RHINOTERMITIDAE
Subfamily HETEROTERMITINAE

Genus *RETICULITERMES* Holmgren, 1913

TYPE SPECIES. *Termes flavipes* Kollar 1837 by subsequent designation; Recent, Holarctic.

Reticulitermes sp.
Figs 21, 26

DESCRIPTION. The species is only known from wing material. Wings elongate, forewing with a length/width ratio of 4–3·3:1. Humeral suture nearly straight in forewing (In.17119, In.64535). Sc + R prominent forming the anterior margin. Rs prominent, close to Sc + R, terminating near

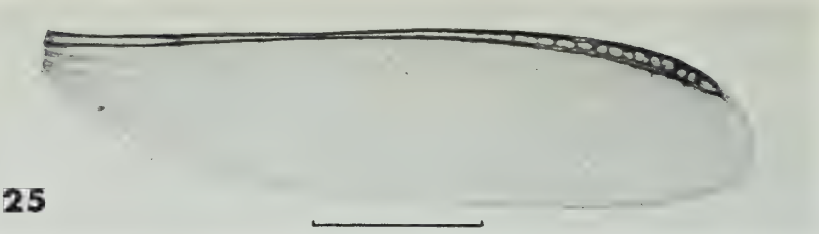


Fig. 25 *Reticulitermes tibialis.* Recent; forewing. Transmitted light. (Scale line = 2 mm)

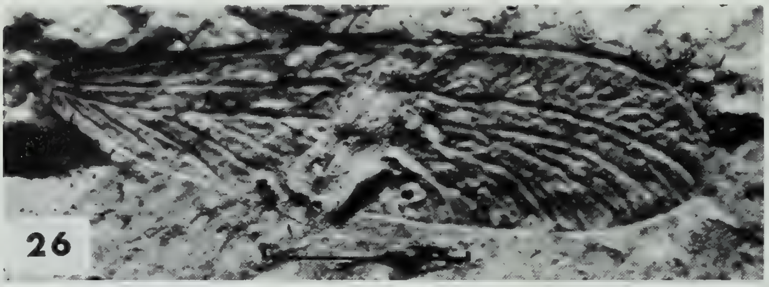


Fig. 26 *Reticulitermes* sp., In.64535. See also Fig. 21. (Scale line = 2 mm)

the wing apex. Cu occupies nearly half the wing width, branching 8–10 times, some branches dividing again distally. M single, closer to Cu than Rs and parallel to the former, with a posterior curve apically.

Membrane reticulate posterior to Rs; a few incipient, transverse ridges may be discernible near the apical extremities of Rs and Sc + R. The reticulation is best developed in the distal part of the Rs space, consisting of oblique transverse ridges tending to join medially to form an irregular longitudinal ridge. Wing colouration : Sc + R and Rs brown along much of their length; Cu and M only pigmented near the suture.

In.24623 and In.25047 are relatively small wings and may represent a separate species.

In.24821 is probably a hindwing as Rs and M appear to meet just distad of the humeral suture and the wing is comparatively narrow near base, but the specimen is too poorly preserved to be referred to this species with certainty.

MATERIAL. Seven specimens and possibly one other.

DIMENSIONS. Forewing length 6·0–6·6 mm, width 1·5–2·0 mm. Length of humeral suture (forewing) 0·5 mm. (In.24623 length 4·5 mm, width 1·3 mm. In.25047 length 5 mm, width 1·4 mm).

REMARKS. The presence of reticulation, a comparatively reduced venation with Rs simple and parallel to the anterior margin, and general habitus place the wings in the Rhinotermitidae : Heterotermitinae. A well-defined, irregular transverse reticulation is like *Reticulitermes* Holmgren (Fig. 25) and unlike *Heterotermes* Froggatt (Banks & Snyder 1920 : 42; Hill 1942 : 121; Weesner 1970 : 495).

Recent *Reticulitermes* spp. are xylophagous insects tunnelling in pieces of damp wood which are frequently buried; adjacent pieces are linked by subterranean galleries (Noirot 1970 : 77). The Pyrsonymphidae, a family of intestinal Protozoa, are confined to *Reticulitermes*. The genus is mainly Holarctic, but there are a few oriental species (Roonwal 1970 : 334). It is essentially temperate; it normally occurs to latitude 46°N in Europe, a little further north than *Kalotermes* (Harris 1970 : 299) and occurs as far south as the borders of Vietnam where it inhabits mountainous regions (Harris 1968).

Family TERMITIDAE

Species A

Figs 14, 35

Description. The material consists of a single wing broken off at the humeral suture. Wing narrow basally, apex rounded; humeral suture short, straight. Sc + R prominent, gently curved. Rs prominent, close and parallel to Sc + R for most of its course terminating just before the wing apex. Rs with a short, forked apical branch, but this is weak and not pigmented like the main stem. M separates from R a short distance beyond the suture; Cu relatively short, terminating near the mid-length of the wing and branching five times. Sc + R, Rs and base of Cu are brown-coloured. There is some faint reticulation of the wing membrane especially near the apex.

Material. In.24603 (H) (Figs 14, 35) and counterpart In.24596 (H).

Dimensions. Maximum length 5·5 mm, width 1·6 mm. M divides 2·0 mm from base.

Remarks. The simple venation, M well separated from Rs and close to Cu, and reduced reticulation are indicative of the higher termites (Termitidae). This is the largest family of Isoptera at the present day and is essentially tropical although some genera range into warm temperate regions (Harris 1970 : 309). Termitids are humivorous or phytophagous, the latter including wood feeders; nesting habits are varied (Noirot 1970).

The wing venation of the fossil approaches that of extant *Apicotermes occultus* Silvestri (Apicotermitinae); the reticulation suggests some affinity with the Macrotermitinae, e.g. *Microtermes* spp. The systematic position of the fossil within the family is uncertain and it may well represent an extinct genus.

Family Uncertain

In.24417 (H). Basal half of a wing, 9 mm long, with only the posterior part preserved, showing part of Cu and several branches. Membrane slightly tuberculate.

I.8648 (B), I.10204 (B), In.24414 (H), In.24612 (H) and counterpart In.25358 (H), In.24616 (H) and In.24618 (H) are indeterminate wing fragments belonging to the Kalotermitidae or Rhinotermitidae.

Order PLECOPTERA
Suborder FILIPALPIA
Family LEUCTRIDAE

Genus *LEUCTRA* Stephens, 1836

Type species. *Phryganea fusca* Linné 1758 by subsequent designation; Recent, Palaearctic.

Leuctra priscula (Cockerell) comb. nov.

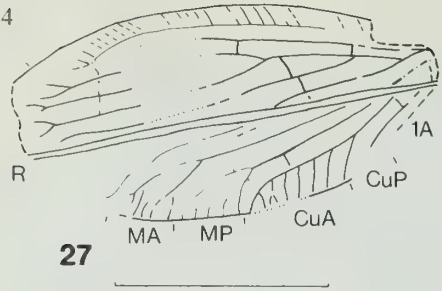
Fig. 22

1922 *Nemoura* (s. lat.) *priscula* Cockerell : 34; fig. 2.

Emended description. Single specimen consisting of an incomplete forewing with the outer half and most of the anterior area preserved. Estimated original length 7 mm. Sc reaches anterior margin 2·75 mm from wing apex. Rs, M and Cu two-branched. Crossvein r–m originating just basad of the fork of Rs, m–cu from M_{3+4} just distad of the fork of M. Four Cu crossveins preserved, the only crossveins apical to the cord. Sc_2 and i.r nearly continuous and perpendicular to anterior margin.

Holotype. In.17498 (S). Fig. 22.

Remarks. The venation is plecopteran of the *Leuctra* type (Needham & Claassen 1925 : pl. 2, fig. 21). It is distinguished from *Nemoura* Latreille by the absence of an oblique crossvein in the apical marginal space (*ibid.* : 196). The fossil is referred to *Leuctra* Stephens *s. lat.*, the material


1A
R
CuP
CuA
MA
MP

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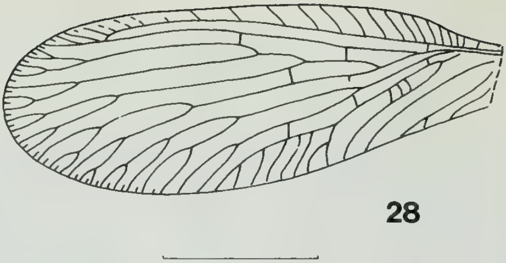

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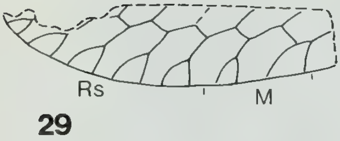

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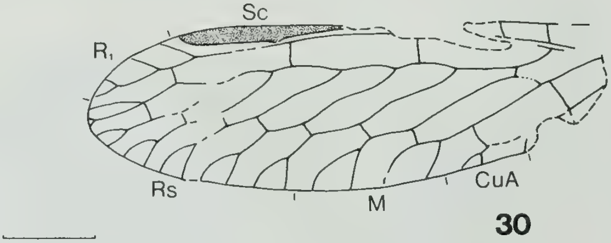
Sc
R1
Rs
M
CuA

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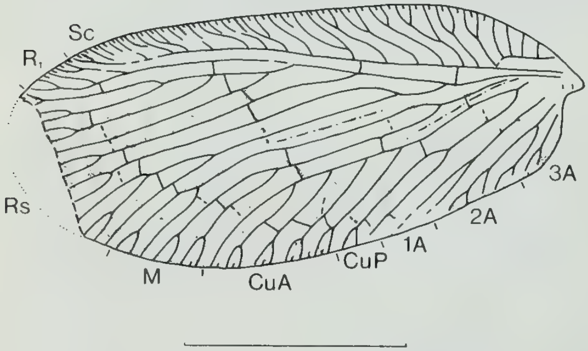
Sc
R1
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1A
2A
3A

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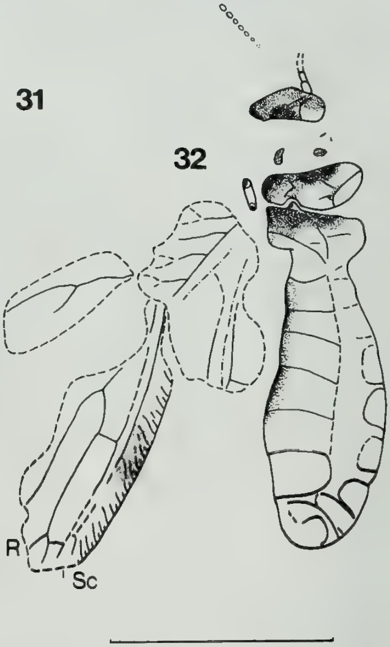

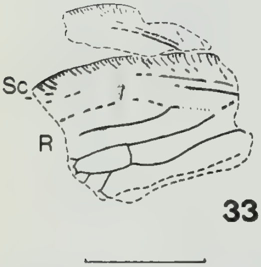

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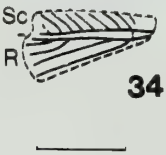

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Fig. 27 Sisyridae species A, forewing. In.17287.

Fig. 28 *Sisyra fuscata* (Fabricius). Recent; forewing.

Figs 29–30 *Promantispa relicta* (Cockerell) gen. and comb. nov. Fig. 29, holotype, In.24326. Fig. 30, In.24597 (forewing).

Fig. 31 *Hemerobius tinctus* n. sp. **Holotype**, I.9160.

Fig. 32 Hemerobiidae species B. The wings are in fact at a slight angle to the body but are drawn as if coplanar. In.17173.

Fig. 33 Hemerobiidae species A. In 43477.

Fig. 34 Hemerobiidae species C. In.17445.

(Scale line = 2 mm)

being too fragmentary for certain reference to any of the subgeneric or generic segregates of *Leuctra* currently recognized by entomologists.

Leuctrid adults are found amongst stones and foliage near freshwater streams, rivers and lakes which are the habitat of the aquatic nymphs. Both adults and young are herbivorous, the former feeding on lichens and small algae (Claassen 1931 : 97; Hynes 1941 : 529, 534, 547–548). The family is mainly Holarctic and the common name of needleflies stems from the adult habit of rolling the wings around the body in repose.

Order **NEUROPTERA**
Family **MANTISPIDAE**

Genus ***PROMANTISPA*** nov.

DIAGNOSIS. A Palaeogene genus of Mantispinae differing from *Mantispa* Illiger in the possession of an apically extended pterostigma.

TYPE SPECIES. *Mantispa relicta* Cockerell 1921*b*.

Promantispa relicta (Cockerell) comb. nov.
Figs 29, 30

1921*b* *Mantispa relicta* Cockerell : 477–478; fig. 46.

EMENDED DESCRIPTION. The original description is based on a single wing fragment 7 mm long, preserving the distal portions of the branches of M and five branches of Rs, plus part of a gradate series of crossveins (Fig. 29). The veins are coloured brown and macrotrichial bases are visible on the veins and wing margin.

The discovery of an unrecognized left forewing (In.24597 + In.24631) requires a redescription of the species. During fossilization, the wing was broadly folded about a longitudinal axis and Fig. 30 is based on a combination of three *camera lucida* drawings from slightly different positions. Original length estimated at 15 mm. Costal area with basal expansion as usual in mantispid forewings, with two well-separated crossveins preserved. Sc curved posteriorly in its apical portion to form the posterior boundary of the pterostigma. The latter is pale brown, very elongate and blunt apically. Sc deflected towards R_1 just distad of 2nd r_1–rs indicating the position of a short pterostigmal crossvein at 0·4 of the length of the pterostigma from base. R_1 on prominent wing fold, close to Sc basally, and producing three oblique crossveins to the anterior margin beyond the pterostigma. Rs undulose, originating 10·0 mm from wing apex, with six branches to the outer posterolateral margin and three equidistant crossveins to R_1 partitioning the branches 1, 2, 2, 1. M dividing nearly opposite R with a short r–m crossvein a small distance distad of the fork; an oblique m–cu just basad of the fork is continuous with an incompletely preserved cubital crossvein. Branches of Rs, M and CuA_1 end-twigged and linked by one gradate series of crossveins; branches of Rs and MA undulose. CuA_2 short and apparently single.

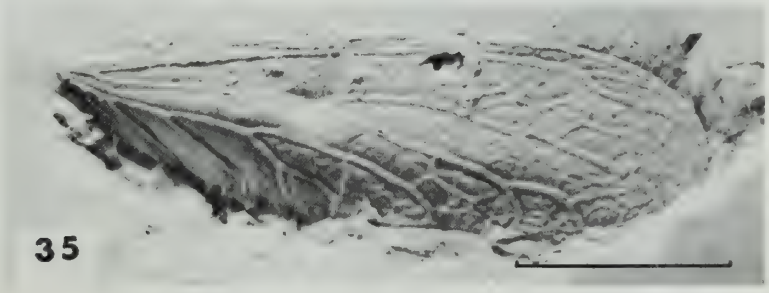

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Fig. 35 Termitidae species A, In.24603. See also Fig. 14. (Scale line = 2 mm)

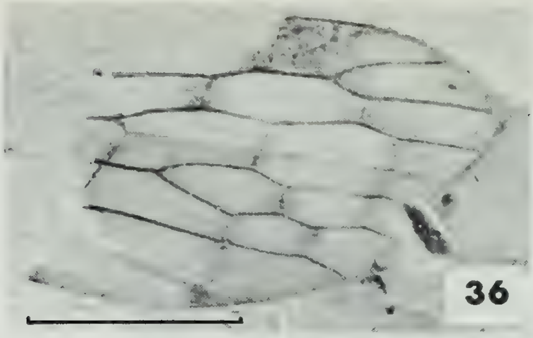


Fig. 36 *Bittacus veternus* (Cockerell) comb. nov. Holotype, In.24330, ventral half. See also Fig. 44. (Scale line = 2 mm)

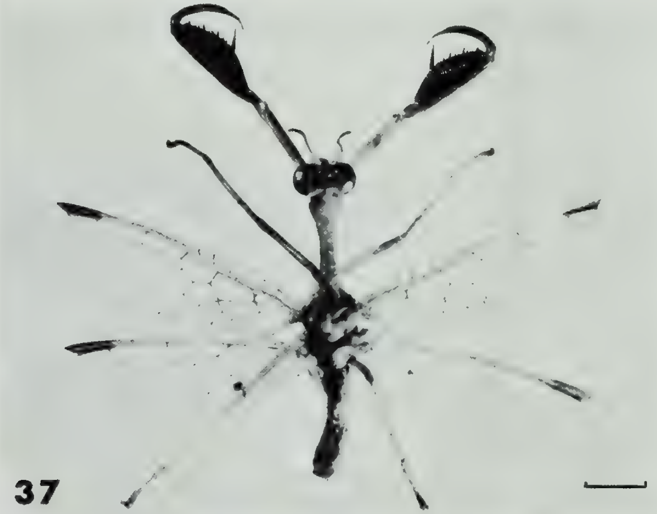


Fig. 37 *Mantispa tenella* Erichson. Recent. (Scale line = 2 mm)

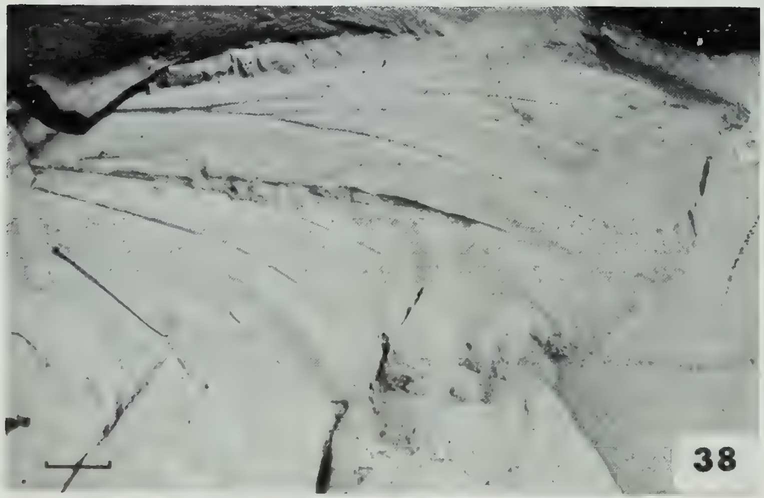


Fig. 38 *Prohepialus* sp., wing. In.17464. (Scale line = 2 mm)

Veins dark brown; macrotrichial bases visible on veins, pterostigma and wing margin; macrotrichial hairs preserved along the margin near the apex. Trichosors absent.

HOLOTYPE. In.24326 (H.15381). Fig. 29.

OTHER MATERIAL. In.24597 (Fig. 30) and incomplete counterpart In.24631 (H).

DIMENSIONS. Forewing: maximum length 11·5 mm, width 3·5 mm.

REMARKS. The *Mantispa*-like venation and absence of trichosors place the fossil in the Mantispidae : Mantispinae (Tjeder 1959 : 275). However, the pterostigma in *Mantispa* is relatively short (Handschin 1959 : 198) and usually has an obliquely truncate apical margin just beyond the pterostigmal crossvein. The pterostigma in the fossil bears some resemblance to *Ditaxis biseriata* (Westwood), but the venation of the latter is quite different. Comparison of the fossil with species representing all the known genera of Mantispidae (about 38) indicates that a new genus is required. *Promantispa relicta* (Cockerell) gen. and comb. nov. appears to be the only known fossil representative of the family.

Recent mantispids (mantis flies) are found in all major regions including Europe, but they no longer occur in Britain. The adults are found on vegetation where they are predacious on other insects, the raptorial forelegs (Fig. 37) having a striking convergence with those of mantids (praying mantises) and berothids (Rachiberothinae). The older larvae of Mantispinae enter the egg sacs of spiders where they feed, hypermetamorphose and pupate (McKeown & Mincham 1948; Tjeder 1959 : 260, 273); the Order Araneida is represented in the Insect Bed.

Family **HEMEROBIIDAE**

Genus ***HEMEROBIUS*** Linné, 1758

TYPE SPECIES. *Hemerobius humulinus* Linné 1758, by subsequent designation; Recent, Holarctic.

Hemerobius tinctus sp. nov.

Fig. 31

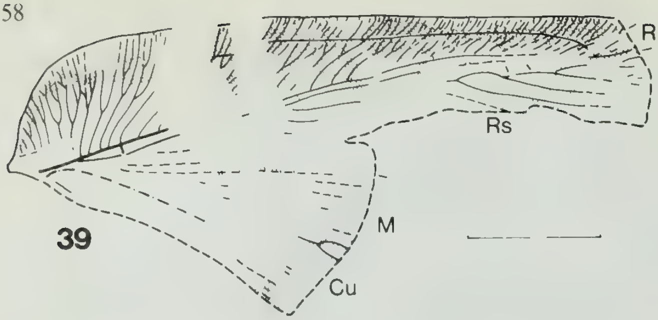
DIAGNOSIS. A Palaeogene species of *Hemerobius* differing from *H. humulinus* in that the inner branch of Rs is divided near base and there is an sc–r crossvein near the base of the middle branch of Rs.

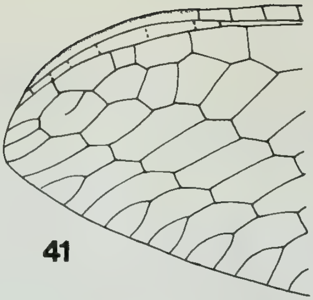
DESCRIPTION. The species is known from a single forewing and is smaller than *Hemerobius humulinus* (Killington 1936 : pl. 13) with an estimated forewing span of 11 mm. Costal area narrow, humeral vein recurved with four single branches to the anterior margin. Sc terminating on anterior margin and branching about 17 times. Rs arising from R on three branches, inner branch dividing close to base and outer branch separating near mid-point of wing; the latter branch with three main forks. Sc linked to stem of R by two crossveins immediately basad of the origins of the middle and inner branches of Rs. No basal r–m nor basal crossvein between the branches of Rs. MA and MP separating near the base of M, forking distally. CuA branching four times distally, CuP with a single fork. Two gradate series of crossveins present, outer series extending from R_1 to 1A. Veins with macrotrichia and usually end-twigged marginally. Trichosors present. Colour pattern consisting of a light brown pigmentation of the membrane especially in the outer part of the wing and tending to form transverse bands.

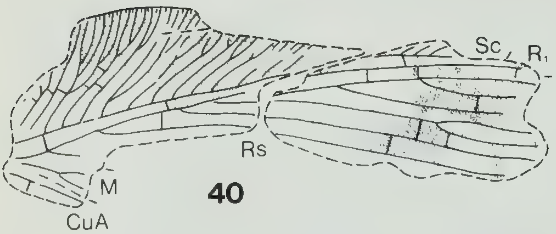
HOLOTYPE. I.9160 (B). Fig. 31.

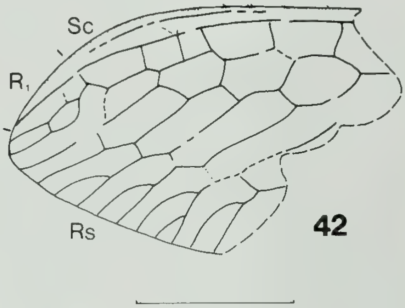
DIMENSIONS. Forewing length 5·0 mm, maximum width 2·2 mm.

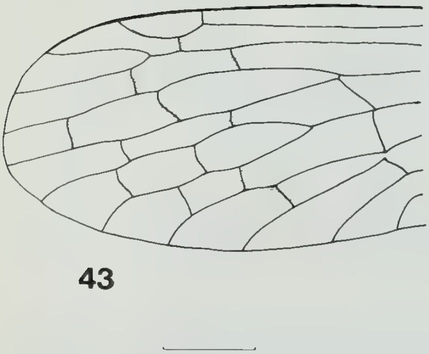
REMARKS. Rs arising on more than two stems, Sc terminating on the costal margin and general form of the wing place it in the family Hemerobiidae (Riek 1970). The fossil is close to the extant *Hemerobius humulinus* (Killington 1936 : fig. 11; pl. 13, fig. 3) but comparison with this and other *Hemerobius* spp. in the BM(NH) indicates that the basal fork of the inner branch of Rs and the

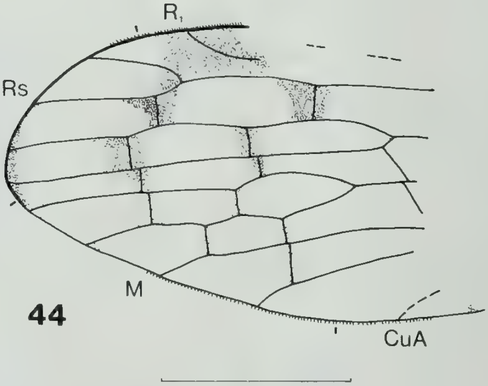


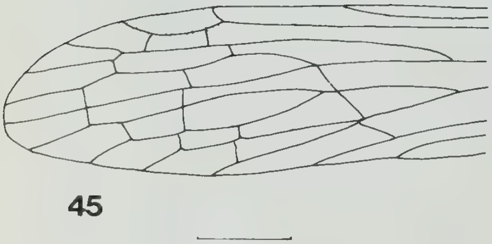



Sc
R₁
Rs
M
CuA
40






R₁
Rs
M
CuA
44



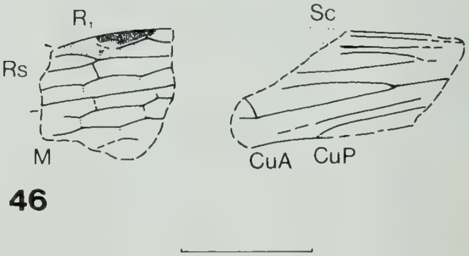

R₁
Rs
M
Sc
CuA
CuP
46

Fig. 39 ? *Neuronema* species A. In.17404.

Fig. 40 ? *Neuronema* species B. In.64536.

Fig. 41 *Nothochrysa capitata* (Fabricius). Recent; hindwing tip. The crossveins in the subcostal space are not prominent and less likely to be preserved if fossilized (cf. Fig. 42).

Fig. 42 Chrysopidae species A. I.8643.

Fig. 43 *Bittacus sinensis* Walker. Recent; forewing tip.

Fig. 44 *Bittacus veternus* (Cockerell) comb. nov. Holotype, In.24330. See also Fig. 36.

Fig. 45 *Bittacus chlorostigma* McLachlan. Recent; outer part of forewing.

Fig. 46 *Bittacus* species A. In.64537.

(Scale line = 2 mm; Figs 39–41 are to same scale.)

crossvein near the base of the middle branch of Rs is unusual for the genus and may form the basis of a supraspecific grouping. The colouration of *H. tinctus* sp. nov. resembles Recent *H. atrifrons* McLachlan.

Recent hemerobiids (brown lacewings) are terrestrial insects and both adults and larvae prey on small soft-bodied arthropods. They are commonly arboreal but also occur on low herbage. The genus *Hemerobius* has a cosmopolitan distribution and can be economically important in the biological control of aphids (Balduf 1939 : 251–253, 256–257, 259; Tjeder 1961 : 296).

Genus *NEURONEMA* McLachlan, 1869

TYPE SPECIES. *Hemerobius decisus* Walker 1860, by original designation; Recent, Hindustan.

? ***Neuronema*** **sp. A**

Fig. 39

DESCRIPTION. The species is known from a single impression of an incomplete left forewing, original length estimated at about 12 mm. Costal area very broad near base, narrowing apically and with a distinctive longitudinal line as in some Recent hemerobiids. Costal crossveins numerous, usually forking once and often twice in their distal halves and becoming increasingly oblique towards apex. The first seven crossveins are evenly truncate at base, indicating the course of a strongly recurved humeral vein, although the vein itself is difficult to discern. Sc and stem of R are marked by strong folds in their proximal portions, flattening out distally and curving towards the apex. Subcostal area with a slight basal expansion. Five branches of Rs can be distinguished and the spacing indicates that this is close to the actual complement. Four to five branches of R_2 are discernible. The median area is bounded by a faint fold on its outer side and a prominent fold on its inner side. M and Cu indicated by some vague traces of venation. Colouration : dark brown mottles in costal area and traces of an oblique brown band across the wing; similar browns are typical in the wing colouration of Recent hemerobiids.

MATERIAL. In.17404 (S). Fig. 39.

DIMENSIONS. Forewing length 10·5 mm, maximum width 4·8 mm.

REMARKS. Rs arising on several branches from R is indicative of the Hemerobiidae (Fraser 1959 : 18; Riek 1970 : 482). The wide costal area, recurved humeral vein, Rs with four to six or seven branches, pectinate branching of R_2 and form of the costal crossveins place the fossil close to Recent *Drepanacra* and *Neuronema* (Nakahara 1960 : 61–62; pls 15–16), especially the latter oriental genus (e.g. *Neuronema irrorata* Kimmins).

Drepanacra Tillyard is an Australian genus and known to feed on *Neomyzaphis* Theobald (Balduf 1939).

? ***Neuronema*** **sp. B**

Fig. 40

DESCRIPTION. The fragmentary forewing is of a similar size and colouration to Species A. The costal area differs in that there are a few longitudinal crossveins towards base. A basal crossvein between Sc and R is present as well as two more apical crossveins. Rs arises on four branches, R_2 with three well-spaced forks. R_4 with basal crossvein to R stem, R_1 with three crossveins to R_2 stem. There are also several crossveins in the apical portions of R_2–R_4. M divides near base.

MATERIAL. In.64536 (E. A. Jarzembowski, J. Cooper and S. F. Morris). Fig. 40.

REMARKS. Species B is close to Species A but differs principally in the presence of the longitudinal crossveins in the costal area and R_2 appears to have fewer branches.

Genus **indet.**

Species A

Fig. 33

DESCRIPTION. The species is known from two fragments of the apico-anterior region of the wings. Forewing: three branches of Rs preserved, the outer branch apparently with only two main forks. Inner gradate series represented by two separate crossveins, the anterior of which is well distad of the above-mentioned forks. Trichosors present. The colouration consists of brown mottles.

MATERIAL. In.43477 (H). Fig. 33.

REMARKS. The fragmentary specimen may well belong to *Hemerobius* but is too incomplete for its generic affinities to be ascertained. The species differs from *H. tinctus* sp. nov. in its larger size (the distance from the origin of the outer branch of Rs to the apical end of Sc is about 3·3 mm compared with 1·7 mm in *H. tinctus* sp. nov.) and position and incompleteness of the inner gradate series.

Species B

Fig. 32

DESCRIPTION. The species is known from a single body impression and forewing fragments. Head wide, with globular eyes and moniliform antennae. The abdominal sclerites are well preserved with a well-defined membranous area between the tergites and sternites, the modification of tergites 8–10 being indicative of a female (cf. Killington 1936 : fig. 13). Forewing: costal area moderately narrow, Rs apparently arising on more than one stem; outer branch of Rs with two main forks and two crossveins to R_1 a little distad of the forks. Trichosors present. The membrane is pigmented light brown in the pterostigmal area.

MATERIAL. In.17173 (S). Fig. 32.

DIMENSIONS. Length of body 4·0 mm.

REMARKS. The generic position of the species is uncertain, like Species A, but it is readily separated from the latter by the wing colour-pattern.

Species C

Fig. 34

DESCRIPTION. Dorsal impression of a fragment of a right forewing from near the base of the wing, maximum length 3·0 mm, width 1·5 mm. Sc on prominent upfold with the bases of eight oblique costal crossveins preserved. Stem of R slightly deflected posteriorly before converging on Sc basally; a transverse groove possibly represents a basal crossvein. Rs represented by four branches with fine parallel folds in the wing membrane between them. Some brownish pigmentation of the veins and membrane.

MATERIAL. In.17445 (B). Fig. 34.

REMARKS. Rs arising on several branches, the basal expansion of the subcostal area and general appearance of the fragment would place it in the Hemerobiidae (cf. corresponding area in Fig. 39, p. 258). The generic affinities of the fragment are indeterminate but size comparison with ? *Neuronema* sp. A indicates a species with probable wing length of about or a little less than two-thirds of the latter.

Family **CHRYSOPIDAE**

Subfamily **CHRYSOPINAE**

Species A

Fig. 42

DESCRIPTION. Dorsal impression of an apical fragment of a right hindwing, maximum width

3·1 mm, length 5 mm. Estimated original length 13–16 mm. Wing membranous; apex pointed, relatively sharp. Macrotrichial bases visible on wing margin and veins, especially numerous along C. Sc marked by prominent fold; Sc and R_1 curved towards apex distally. Rs zigzagged, with eight branches preserved, the basal four showing end-twigging. Rs linked to R_1 by a number of crossveins; branches of Rs joined by two series of gradate crossveins.

MATERIAL. I.8643 (B). Fig. 42.

REMARKS. R_1 distinct from Rs but linked by numerous crossveins, branches of Rs arising from a single (zigzagged) stem and the absence of trichosors are characteristic of Chrysopidae (Fraser 1959 : 15; Riek 1970 : 482). The reduced venation excludes the fossil from the Apochrysinae (cf. Kimmins 1952) and places it in the Chrysopinae in the wider sense (Riek 1970). The specimen is too fragmentary for more detailed determination. A Recent wing is illustrated in Fig. 41 for general comparison.

Recent chrysopids (green lacewings, etc.) are found in both warm and temperate regions of the world (Tjeder 1966 : 243). The larvae and adults (Chrysopinae *s. lat.*) are predominantly arboreal although they also occur on low vegetation, where the larvae and many of the adults prey on small, soft-bodied arthropods, mainly insects (Balduf 1939 : 271–272, 291; Tjeder 1966 : 228).

Family **SISYRIDAE**

Species A

Fig. 27

DESCRIPTION. The species is known from a single left forewing, estimated original length 5·0 mm. The wing has been folded longitudinally in two upon itself, but the two halves are readily distinguished by (a) the general orientation of the veins and (b) the veins of the anterior portion being convex and ridge-like and the posterior ones concave since they are seen from the underside. Costal area moderately wide, macrotrichial bases visible along the anterior margin and on some crossveins. Sc curved towards R_1 apically, costal crossveins numerous, unforked. R forked near wing base, R_1 parallel to Sc basally but not preserved apically. Rs branching four times with R_2 apparently divided. Short inner gradate series of crossveins present and traces of an outer series. MA and MP divided apically, branches forked. CuA with seven short distal branches, the latter simple except for one which appears to be forked. CuA linked by prominent crossveins to CuP basally and MP apically. Colouration: veins and pterostigmal area light brown. The membrane shows traces of a similar pigmentation in the middle and outer parts of the wing.

MATERIAL. In.17287 (S). Fig. 27.

REMARKS. The wing form and venation of the fossil are closest to the extant genus *Sisyra* Burmeister (Fig. 28); Sc curving to terminate on R_1 distally is typically sisyrid (Nakahara 1958). The inner gradate series resembles that of *Sisyra panama* Parfin & Gurney and the fork of R_2 is similar to *S. vicaria* (Walker). Comparison with Recent species in the BM(NH) shows that the fossil differs from *Sisyra* in that the costal crossveins and branches of CuA are more numerous and the apical r_1–rs crossvein appears to be immediately below rather than beyond the termination of Sc. The branching of CuA is more like the Nearctic sisyrid *Climacia areolaris* (Hagen) and the costal crossveins resemble *Neurorthus* spp. The Neurorthinae have been removed from the Sisyridae in recent years and elevated to family rank (Zwick 1967). The larvae of both families live in fresh water except those of *Austroneurorthus* Nakahara which probably inhabit damp places; adults are found near the larval habitat. The Sisyridae have a cosmopolitan distribution and the larvae are parasitic on fresh-water sponges (Porifera : Spongillidae) (Parfin & Gurney 1956; Zwick 1967; Riek 1970). Both neurorthids and sisyrids are known in the Baltic amber and a number of specimens await description (Macleod 1970). The systematic position of the amber 'sisyrid' *Rophalis relicta* Hagen is unsettled (Parfin & Gurney 1956; Nakahara 1958).

Family Uncertain

In.20557 (B). Fragment probably of the costal area of a wing, preserving a straight portion of the wing margin and distal parts of 22 crossveins. Length 5 mm, width 1 mm. Crossveins slightly inclined to the margin, evenly spaced, and single except for one with a terminal fork. Macrotrichial bases dense on wing margin and also evident along the veins, no trichosors. Membrane pale brown, veins and margin dark brown.

Order **MECOPTERA**
Suborder **EUMECOPTERA**
Family **BITTACIDAE**

Genus ***BITTACUS*** Latreille, 1805

Type species. *Panorpa italica* Müller 1766, by subsequent designation; Recent, western Palaearctic.

Bittacus veternus (Cockerell) comb. nov.

Figs 36, 44

1921*b* *Panorpa veterna* Cockerell : 478; fig. 47.

Emended description. The species is known from the apical part of a right wing, original length estimated at 12–14 mm. Wing membranous, slightly folded about R_5. Macrotrichia visible along part of anterior and posterolateral margins. R_1 represented by the curved apical end; Rs four-branched, R_{4+5} forking 4 mm from wing apex, R_{2+3} opposite the end of R_1. R_{3-5} linked to each other by two transverse crossveins. M four-branched, M_{1+2} forking a little nearer the apex than R_{4+5}; M_3 and M_4 converging but fork not preserved. First r–m oblique, originating close to the base of R_5; 1st i.m. also oblique commencing near the end of the r–m but is incompletely preserved. R_5 and M_{1-3} are also linked to each other by two transverse crossveins with one to M_4. CuA represented by a small apical fragment. Wing colouration: veins brown; dark brown areas around the end of R_1 (pterostigma) and the transverse R crossveins; paler brown around the transverse M crossveins. Wing tip also dark. The pigmentation is similar in colour to Recent Mecoptera.

Holotype. In.24330, with counterpart (H). Figs 36, 44.

Dimensions. Maximum width 3 mm, length 5 mm.

Remarks. The reduced venation excludes the fossil from Meropeidae and Notiothaumidae (Grassé 1951 : 107) and places it in the Eumecoptera. Cockerell (1921*b*) stated that it resembles the living *Panorpa germanica* L. (Panorpidae) except in details of colour pattern. I have examined a series of specimens of this European species in the museum collection, and in addition the fossil differs in that R_2 is short and does not fork and that 1st r–m is more or less continuous with 1st i.m. which is directed towards the anastomosis of M_{3+4}. In *P. germanica*, and *Panorpa* Linné in general, R_2 is usually forked (Carpenter 1931 : 213) although there are exceptions. Comparison of *P. germanica* with other panorpid species, e.g. in Esben-Petersen (1921), suggests that 1st i.m. is not normally present close to 1st r–m and fork M_{3+4} is more basal in Panorpidae.

The venation of the fossil in fact agrees best with that of the Bittacidae (Esben-Petersen 1921 : 115–162), and I have compared the specimen with published accounts of the type species of the 12 currently recognized bittacid genera, as well as some additional species in the larger genera (*Bittacus*, *Harpobittacus* Gerstaecker). The shape and venation compares well with *Austrobittacus* Riek, *Bittacus* (e.g. *B. sinensis* Walker, Fig. 43), *Kalobittacus* Esben-Petersen, and possibly *Tytthobittacus* Smithers. The absence of pterostigmal crossveins in the fossil could be preservational failure, as these may be faint in Recent specimens, and are sometimes obscure (Esben-Petersen 1921 : 127). The size corresponds to more than one of these genera: in *Bittacus* a Baltic amber species, *B. minutus* Carpenter, has wings of 3 × 11·5–13 mm. The Bembridge Marls species approaches the living *B. marginatus* Mikayé in the pigmentation of the pterostigma, apex and more apical crossveins, and is provisionally referred to the genus *Bittacus* Latreille.

Recent bittacids (hanging flies) are found on vegetation in sheltered places and are predacious on other insects. The larvae are ground-dwelling scavengers, pupating beneath the surface (Grassé 1951; Byers 1971). The family is temperate–tropical (Carpenter 1931 : 206) with a world-wide distribution except for the northern parts of Europe, Asia and America (Esben-Petersen 1921 : 116). It is no longer found in Britain (Fraser 1959) although represented on the continent (Grassé 1951).

***Bittacus* sp. A**

Fig. 46

Description. The species is known from a single ventral impression of an incomplete left wing without counterpart, of which pieces have flaked away and are not preserved. Original length estimated at *c.* 15 mm. The anterior and posterior margins are sufficiently well preserved to indicate a narrow elongate wing. The longitudinal veins are distinct, but some of the crossveins cannot be discerned although their positions are indicated by the undulations in R and M. R_1, R_5 and CuA are on prominent upfolds. Sc is close to anterior margin in the basal part of the wing, continuing beyond the fork of Rs. R_1 curved posteriorly at its distal end bounding the pterostigma on its posterior side. No definite traces of pterostigmal crossveins. Rs forking just basad of M, the former four-branched and the latter with only three branches preserved. R_3–M_3 interlinked by well-spaced crossveins; 1st i.m. oblique and well distad of the termination of CuP on the posterior margin. Wing colouration: veins brown, pterostigma dark brown; a slightly lighter brown area between R_1 and Rs immediately beneath and distad of pterostigma.

Material. In.64537 (H). Fig. 46.

Dimensions. Maximum length 6.5 mm, width 1 mm.

Remarks. The elongate form and well-developed pterostigma are typically bittacid (cf. Setty 1940 : 282). The venation is close to that of *Bittacus veternus* (Cockerell) comb. nov. but it differs from the latter in that the pigmentation is confined to the pterostigma and adjacent membrane. The wing details agree with Recent *Bittacus* (Fig. 45), but in the absence of further information on this species it can only be referred to this genus in the wider sense.

Order **LEPIDOPTERA**
Suborder **ZEUGLOPTERA**
Family **MICROPTERIGIDAE**

Genus ***MICROPTERIX*** Hübner, 1825

Type species. *Tinea podevinella* Hübner 1813, by subsequent designation; Recent, western Palaearctic.

Micropterix anglica sp. nov.

Fig. 49

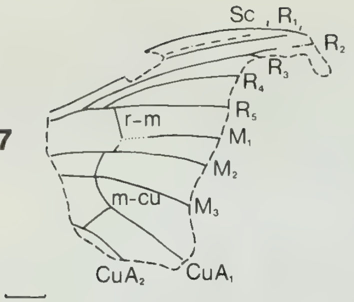
Diagnosis. A Palaeogene species of *Micropterix* with Sc forking distally beyond the origin of R_1 and R_1 unbranched in the forewing.

Description. The single known specimen consists of the greater part of a forewing, original length estimated at about 4 mm. Sc forked, R_1 simple. R_2 and R_3 originating from the outer half of the areole, chorda faintly preserved. R_4 and R_5 single, and like M_1, converging on the apical end of the areole; forks of M_{2+3} and CuA_{1+2} approximately beneath the basal end of the areole. CuP single. 1A represented by a short distal portion. Crossvein r–m faint but no trace of sc–r nor m–cu. Colouration: veins mostly dark brown with intervening membrane light brown.

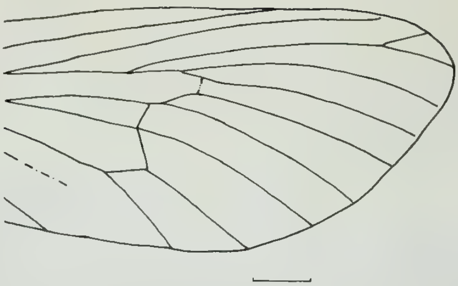
Holotype. In.17411 (S). Fig. 49.

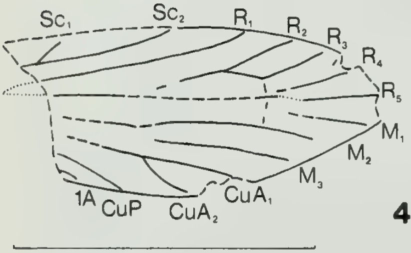
Dimensions. Forewing: preserved length 2·4 mm, width 1·1 mm; length of Sc_2 0·93 mm.

47

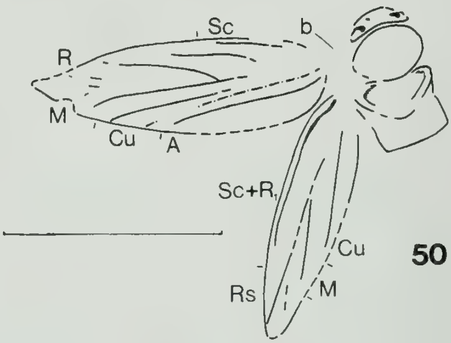

Sc
R_1
R_2
R_3
R_4
R_5
r–m
M_1
M_2
m–cu
M_3
CuA_2
CuA_1

48

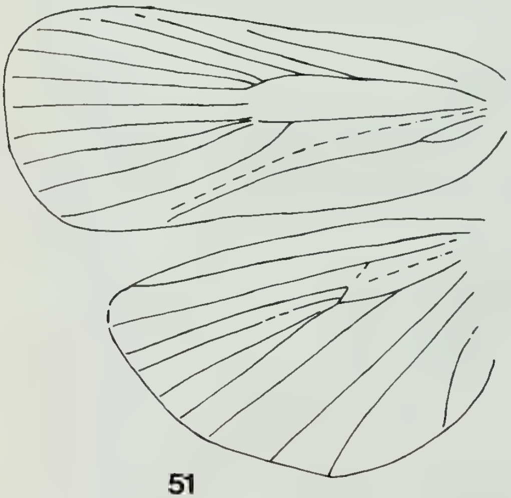



Sc_1
Sc_2
R_1
R_2
R_3
R_4
R_5
M_1
M_2
M_3
CuA_1
1A
CuP
CuA_2

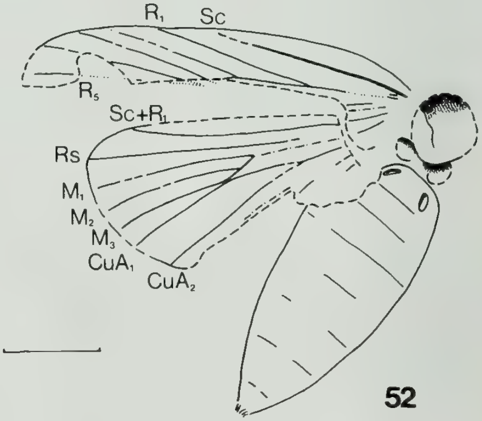
49


Sc
b
R
M
Cu
A
Sc+R_1
Cu
Rs
M

50



51


R_1
Sc
R_5
Sc+R_1
Rs
M_1
M_2
M_3
CuA_1
CuA_2

52

Fig. 47 *Prohepialus* sp. Composite drawing of wing In.64528 (i–iii).
Fig. 48 *Hepialus fusconebulosa* (De Geer). Recent, Britain. Outer part of forewing.
Fig. 49 *Micropterix anglica* sp. nov. **Holotype**, In.17411.
Fig. 50 Microlepidoptera family uncertain sp. A, I.9492. (b = bristle).
Fig. 51 *Copromorpha gypsota* Meyrick. Recent, Fiji. Wing venation.
Fig. 52 *Copromorpha fossilis* sp. nov. **Holotype**, In.25766.
(Scale line = 2 mm. Figs 51–52 are to same scale.)

REMARKS. The homoneurous type of venation and vein details agree with the extant genus *Micropterix*. The absence of crossveins sc–r and m–cu is probably due to preservational failure, as they may be weakly developed in Recent micropterigids. The fossil differs from '*Micropterix*' *proavitella* Rebel (Baltic amber) in that Sc forks more apically and R_1 is unbranched (cf. Rebel 1935 : fig. 17). It approaches the Recent British species *Micropterix* [= *Eriocephala*] *calthella* (Linné) but differs principally in that Sc_1 is shorter and appears to originate more apically of the origin of R_1 compared with the latter (cf. Meyrick 1928 : figure on p. 873).

Recent micropterigids have a widespread distribution but *Micropterix* is confined to the Palaearctic Region. This primitive family includes the earliest known Lepidoptera, from the Lower Cretaceous of Lebanon (Whalley 1977). They are small, metallic-coloured, largely diurnal moths with functional mandibles and no proboscis, feeding on pollen grains; the larvae are considered to feed on bryophytes but some may be detritus feeders (Common 1970). Adult *Micropterix* visit blossoms including *Carex* L. and *Ranunculus* L., both genera being represented in the Insect Bed.

Suborder **EXOPORIA**
Superfamily **HEPIALOIDEA**
Family **HEPIALIDAE**

Genus ***PROHEPIALUS*** Piton, 1940

TYPE SPECIES. *Prohepialus incertus* Piton 1940, by monotypy; Palaeocene, Menat (Puy-de-Dôme).

Prohepialus sp.
Figs 38, 47, 59

1976 hepialid, Jarzembowski : 13.
1977 hepialid, Robinson : 108; figs 5–6.

DESCRIPTION. The material consists of four incomplete wings, estimated wing length 20–45 mm. Sc marked by prominent fold, close to R_1 distally and like R_1 continuing well beyond the end of the discal cell. R_{2+3} closer to R_4 than R_1 at base. Base of R_4 well separated from origin of r–m. Discal cell widening towards apex, M bifurcate in cell. The distance from posterior end i.m. to the anterior end r–m is 0·6 of width of the discal cell across apical angles. R_{2+3} forking beyond the cell at *c.* 1·3 of maximum width of the latter; M_1 + r–m and CuA_1 + m–cu form outwardly-directed angles from the apical end of the cell. Crossvein i.m. oblique, originating from the fork of M_{1+2} or a little basad of the fork. No colour pattern is preserved, but the wing surface has a brownish tinge in some of the specimens because of the presence of scales. In.64528(i) shows numerous oblong scales, but the counterparts, In.64528(ii–iii), show longer forms. Fold Sc is convex in the part indicating that this is the dorsal impression of the wing with scales from the same surface; the counterparts therefore show the ventral scales. Adpressed marginal scales can be seen in In.64528(iii) and In.64538 + counterpart, the latter also with long scales on both surfaces.

MATERIAL. In.17464 (Fig. 38); In.64528(i) and fragments of counterpart In.64528(ii–iii) (Fig. 47); In.64538 (Fig. 59) and counterpart on reverse of In.64528(ii); In.64539 (H).

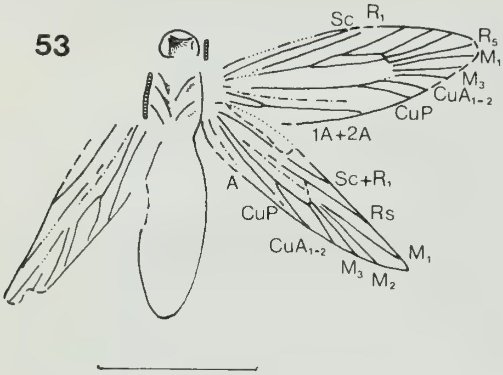
DIMENSIONS. Width of discal cell across apical angles 9·8–*c.* 4·4 mm (In.64538–9).

REMARKS. The general habitus of the wings is indicative of the Hepialoidea, and M forked in the discal cell, m–cu (M_4 *auctt.*) oblique, and comparatively large size place them in the Hepialidae, commonly known as swift moths (Common 1970 : 787, 789). Relationships with Recent genera are uncertain, but the *Hepialus*-like venation (cf. Fig. 48) agrees with the Palaeogene genus *Prohepialus* Piton. The latter genus is based on a single specimen of which the venational details are incompletely known, rendering specific comparison impossible.

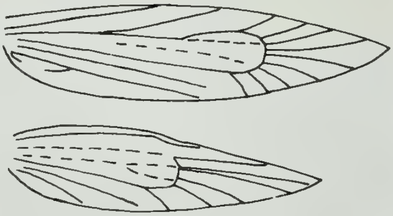
The hindwings of *Hepialus* spp. are slightly smaller than the forewings and this would increase the total variation in wing size. In.64538 and In.64528 could be the fore- and hindwings of the same individual as they come from the same piece of rock, both show traces of pigmented scales, and the difference in size of the discal cell (apical width differs by *c.* 33 %) is within the range of some Recent hepialid specimens. Examination of both surfaces of the forewing of the Recent British *Hepialus fusconebulosa* (De Geer) (Fig. 48) showed a similar shape difference in the scales as in In.64528, and the presence of long scales in the hindwing as in In.64538 + counterpart. The presence of broad longitudinal ridges as well as more numerous, finer ridges is a feature of hepialid scales that was noted by early workers (e.g. Kellogg 1894 : 80–82); both types of longitudinal ridge and other ultrastructural details are preserved in the scale shown in Fig. 59.

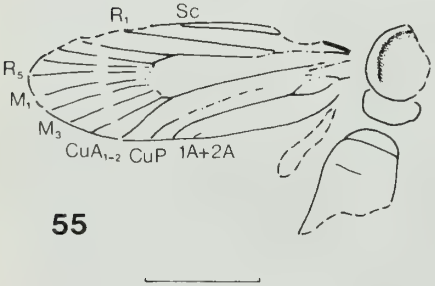
The family has a cosmopolitan distribution but is most diverse in the southern hemisphere. The larvae are phytophagous, tunnelling in wood or soil; the adults are short-lived with mouthparts more or less reduced and functionless (Bourgogne 1951 : 372; Common 1970 : 787).

53

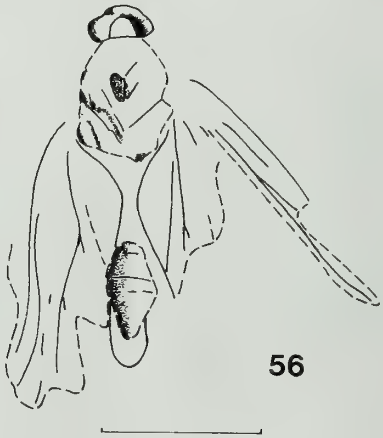

Sc
R₁
R₅
M₁
M₃
CuA₁₋₂
CuP
1A+2A
Sc+R₁
A
Rs
CuP
CuA₁₋₂
M₁
M₃
M₂

54

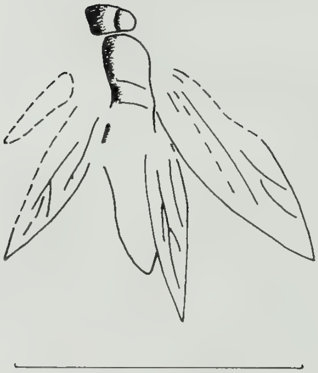



R₁
Sc
R₅
M₁
M₃
CuA₁₋₂
CuP
1A+2A

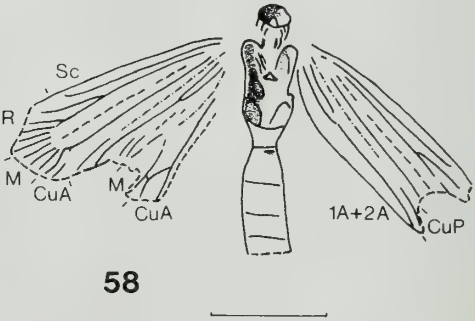
55



56



57


Sc
R
M
CuA
M
CuA
1A+2A
CuP

58

Fig. 53 *Paratriaxomasia solentensis* gen. et sp. nov. **Holotype**, I.9166.

Fig. 54 *Triaxomasia caprimulgella* (Stainton). Recent, Europe. Wing venation, after Zagulyaev (1964).

Fig. 55 Tineidae species A. I.9614.

Fig. 56 Gelechioidea species A. I.9042.

Figs 57–58 Microlepidoptera family uncertain. Fig. 57, species C. In.25512 + In.25252. Fig. 58, species K. In.25219.

(Scale line = 2 mm)

Suborder **DITRYSIA**
Superfamily **TINEOIDEA**
Family **TINEIDAE**

Genus ***PARATRIAXOMASIA*** nov.

DIAGNOSIS. A Palaeogene genus of Tineidae approaching the extant genus *Triaxomasia* Zagulyaev but differing in that the forewing is slightly broader and the hindwing lacks a marginal indentation near the termination of $Sc+R_1$ and is slightly narrower towards base.

TYPE SPECIES. *Paratriaxomasia solentensis* gen. et sp. nov.

Paratriaxomasia solentensis gen. et sp. nov.
Fig. 53

DIAGNOSIS. Species of *Paratriaxomasia* with a forewing span of 8·0 mm.

DESCRIPTION. The species is known from a single ventral impression of the body and wings. Head rounded anteriorly. Forewing approximately three times as long as broad, attenuated apically. Sc close to anterior margin terminating opposite the origin of R_2. R_1 originating a short distance from wing base at about 0·25 of the length of the discal cell. Areole elongate, 0·4 of the

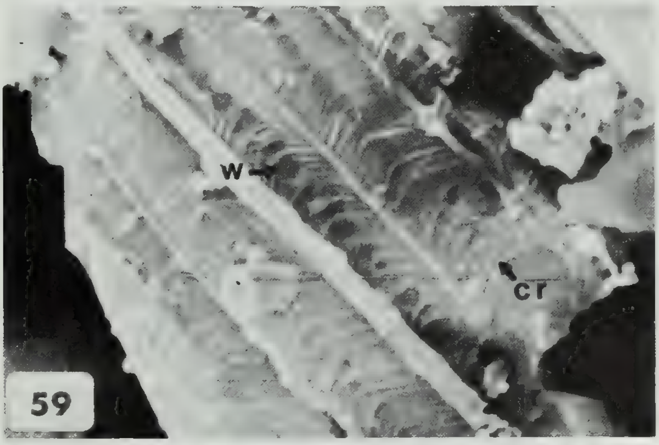


Fig. 59 *Prohepialus* sp., In.64538 (scale, ×10 000; lr longitudinal ridge, cr cross rib, w window).

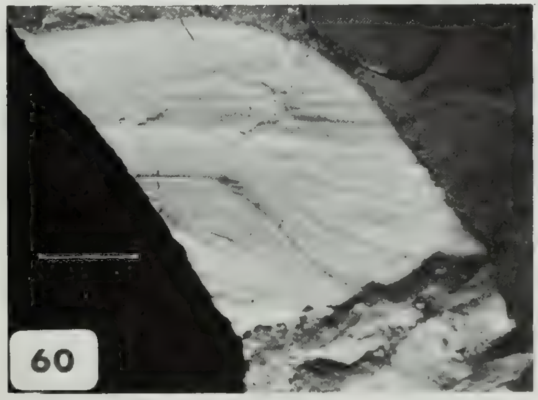


Fig. 60 *Gurnetia durranti* Cockerell, holotype. In.24324. See also Fig. 66. (Scale line = 2 mm)

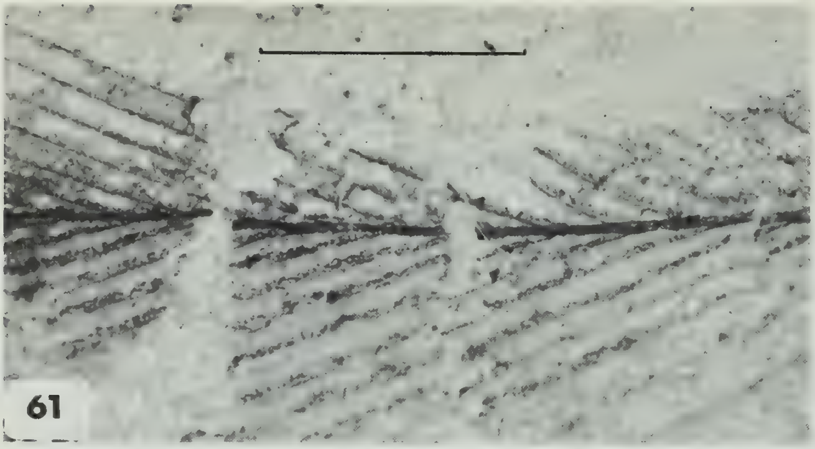


Fig. 61 Fragment of small bird feather, occurring on slab In.17194. See p. 239. (Scale line = 2 mm)

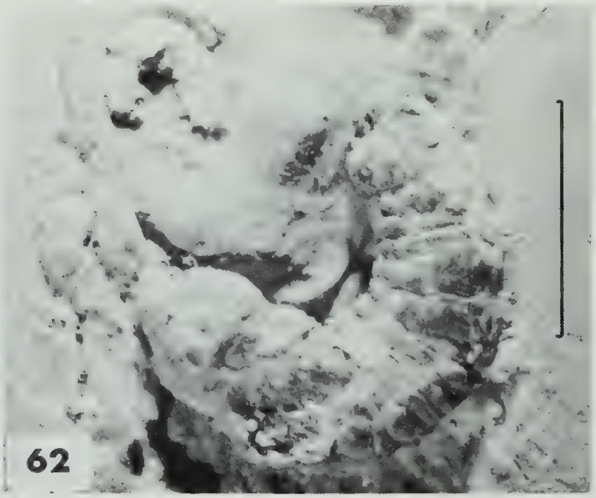


Fig. 62 Insect larvae inside cavity of a plant stem. In.64544. See p. 241. (Scale line = 2 mm)

cell length; R_3–R_5, M_1–M_3 and CuA_1–CuA_2 originating from the apical part of the cell, the origin of R_2 basad of that of CuA_2. R_5 appears to terminate immediately anterior to the wing apex. Hindwing lanceolate, 4·5 times longer than broad and gradually tapering towards the apex. $Sc + R_1$ well separated from the anterior margin, terminating at midlength of wing opposite the apical end of the discal cell. M_1 towards apex, converging on M_2 basally and continuing as a fold into the discal cell. M_3 originating close to M_2 and CuA_1. CuP prominent, anal vein present. Stem of CuA well separated from the posterior margin.

HOLOTYPE. I.9166 (B). Fig. 53.

DIMENSIONS. Length of body 3·6 mm, forewing 3·6 mm and hindwing 3·3 mm.

REMARKS. The wings resemble those of the extant monotypic genus *Triaxomasia* (Fig. 54), from which they differ in that the forewing is slightly broader, there is no faint trace of M in the discal cell and the chorda and 2A appear to be stronger veins; the hindwing is narrower basally, and there is no shallow indentation on the anterior margin near the distal end of $Sc + R_1$ as in

Triaxomera Zagulyaev. The forewing span of the European *Triaxomasia caprimulgella* (Stainton) (Fig. 54) is 10·5–11·5 mm, and like other Nemapogoninae, it is a forest dweller and the larvae are fungus feeders. The caterpillars of this species inhabit fungus-infested rotten wood including *Fagus* L., *Ulmus* L. and *Quercus* L. (Zagulyaev 1964 : 86, 133, 155–160).

Genus **indet.**

Species A

Fig. 55

Description. The species is known from a single specimen with thorax, basal part of abdomen and a single forewing preserved. Meso- and metathorax distinct. Forewing elongate, about three times as long as broad, apex bluntly angular; membrane with distinct transverse lineation. Discal cell elongate, 0·6 of wing length. Sc close to anterior margin, terminating near middle of wing. R_1 originating at a quarter of wing length from base, terminating a short distance beyond the apical end of the discal cell. Branches of R, M and CuA originating relatively close to each other, R_5 towards apex; origin of R_2 a little more basad in position than that of CuA_2 and marking an anterior deflection in the stem of R. Discocellular crossveins indistinct. Chorda apparently absent, but preservational failure in the discocellulars raises the possibility that a weak chorda was present in life. 1A+2A with a short basal loop and well separated from the posterior margin.

Material. I.9614 (B). Fig. 55.

Dimensions. Length of thorax 1·8 mm. Length of forewing 5·8 mm, maximum width of forewing 2·0 mm.

Remarks. The forewing bears some resemblance to that of the incurvariine *Adela reamurella* (Linné) but differs notably in that the apex is more rounded and there is a wider area between the apical end of the discal cell and the outer margin (cf. Meyrick 1928 : figure on p. 843). It is similar in size and form to *Tinea pellionella* (Linné) (cf. Forbes 1923 : fig. 73) although in the latter the forewing is more elongate (about four times as long as broad) and a chorda is present. The venation is also close to that of *Nemapogon granella* (L.) in which the chorda is faint (Forbes 1923 : fig. 74, *Tinea granella* (L.)) and the fossil apparently belongs in the Tineidae, a widespread present-day family.

Superfamily **GELECHIOIDEA**

Species A

Fig. 56

Description. The single specimen consists of a ventral impression of the body, incomplete hindwings and part of the right forewing. The last shows portions of Sc and R, the latter with two well-spaced branches. Hindwing: moderately wide, $Sc+R_1$ and Rs sinuous and preserved in the left wing only; CuA preserved in both wings, CuP prominent, anal area broad, angular.

Material. I.9042 (B). Fig. 56.

Dimensions. Length of body 4·5 mm.

Remarks. Although the fossil is rather fragmentary, the hindwing form and venation resemble some extant gelechiids including *Agnippe* sp. (Brues, Melander & Carpenter 1954: fig. 421), *Parachronistis albiceps* (Zeller) (Spuler 1913 : fig. 123) and *Polyhymno luteostrigella* Chambers (Forbes 1923 : 256). It is tentatively referred to the Gelechioidea. The superfamily has a cosmopolitan distribution; the larvae are usually phytophagous.

Superfamily COPROMORPHOIDEA
Family COPROMORPHIDAE

Genus *COPROMORPHA* Meyrick, 1886

TYPE SPECIES. *Copromorpha gypsota* Meyrick 1886, by monotypy; Recent, Australian Region (Pacific).

Copromorpha fossilis sp. nov.
Fig. 52

DIAGNOSIS. A Palaeogene species differing from the living *C. gypsota* in the smaller size of the wings, the slightly more basad termination of the branches of R in the forewing, and M_1 closer to Rs in the hindwing.

DESCRIPTION. The single specimen consists of the dorsal impression of a decapitated body and the remains of the right wing pair.

Body: posterior end of mesothorax rounded, metascutum distinct. Abdomen completely flattened except for two lateral cavities in the basal segment; seven annuli are discernible and the remains of the apical scale cover. The abdomen is comparatively large even allowing for compression and, together with the pointed posterior, suggests that the holotype is a female.

Forewing: anterior margin rounded basally, straightening distad of the termination of Sc and curving strongly past R_4. Sc terminating near the mid-length of the wing; R_1 originating at 0·25 and terminating at 0·65 of the forewing length (from base); R_3 and R_4 terminating at 0·85 and 0·94 of the same length. Base of R_2 well separated from that of R_1. CuA, 1A and 2A represented by short basal portions close to the CuP fold; anal veins well separated from the margin.

Hindwing: apex rounded with an angle of 85°. Anterior margin straight, outer margin curving gently towards base away from the apex. $Sc+R_1$ elongate continuing apically well beyond the end of the discal cell. Rs directed towards apex. Bases of M_1–M_3 linked by oblique crossveins. M_2 equidistant between M_1 and M_3, M_1 continuing as a distinct fold in the discal cell. Base of M_3 touching CuA_1 at 0·4 of its length from the separation of CuA_2.

HOLOTYPE. In.25766 (H). Fig. 52.

DIMENSIONS. Length of forewing 8·8 mm.

REMARKS. The wing form and venation come closest to that of extant moths of the family Copromorphidae and the type genus itself (Fig. 51). The genitalia of Copromorphoids show affinities with those of the Gelechioidea and the venation of the fossil shows some resemblance to the Oecophoridae. Although the bases of R_4 and R_5 are not preserved, their courses indicate that they do not form a distinct fork as is characteristic of the Oecophoridae. The apical angle is close to 90°, in agreement with the Copromorphidae.

The family has a southern distribution, only *Aegidomorpha* Meyrick entering the Palaearctic in China; *Copromorpha* occurs in Africa and from India through to Australia. Copromorphid larvae are tunnellers in leaf veins, twigs and fruits (Common 1970 : 827).

Microlepidoptera, Family uncertain

Species A
Fig. 50

DESCRIPTION. The species is known from the dorsal impression of a single specimen with the left pair of wings and anterior part of the body preserved. Estimated wing span 6·0 mm. Body pale brown; base of abdomen, meso- and metathorax distinct but dorsoventrally compressed. Head rounded anteriorly. Wings elongate, apices pointed, with some scale traces.

Forewing: broader and slightly longer than hindwing. Anal area broad, CuP marked by a prominent fold terminating on the posterior margin at 0·6 of the wing length from base; Sc close to anterior margin and terminating at 0·4 of the same length. Distal part of stem R + M preserved close to CuA; two branches of R well defined as in Fig. 50 and apical venation suggested by some faint traces. CuA and A single and close to CuP fold.

Hindwing: $Sc + R_1$ thickened basally, long and close to anterior margin: a detached bristle may represent the frenulum. Rs + M forking near mid-length of wing; Cu single.

MATERIAL. I.9492 (B). Fig. 50.

DIMENSIONS. Forewing length 2·7 mm; hindwing length 2·3 mm.

REMARKS. The venation approaches that of the modern leaf-miners *Heliozela* Herrich Schaffer (Common 1970 : fig. 36.15B) and *Nepticula* Heyden (*N. terminella* Braun ♀, Forbes 1923 : fig. 56), and Species A probably belongs in either the Incurvariina or Nannolepidoptera.

Species B

DESCRIPTION. The species is known from a single specimen consisting of the ventral impression of the body plus forewings. Estimated wing expanse 6·0 mm. Body elongate, head well rounded anteriorly. Forewing lanceolate, with some traces of scale cover. Sc close to but well separated from anterior margin, probably not continuing beyond mid-length of wing. Anal area broad, CuP fold prominent. Stem of R + M close to CuA; R producing three branches to the anterior margin in outer half of wing, some faint suggestions of venation posterior to last branch. Vein A single, and like the stem of CuA, close to CuP fold.

MATERIAL. In.64540 (H).

DIMENSIONS. Body length 2·8 mm, forewing length 2·7 mm.

REMARKS. The forewing venation comes close to that of *Heliozela* but also resembles the gelechioid *Dyselachista sericiella* (Haworth) [=*saltatricella* (Fischer von Röslerstamm)] (cf. Spuler 1913) and the lyonetiid *Leucoptera laburnella* (Stainton) (cf. Meyrick 1928); the exact affinities are uncertain. The latter two species are a little larger than Species B.

Species C
Fig. 57

DESCRIPTION. A very small moth with an estimated wing expanse of about 3·8 mm. Head rounded anteriorly. Mesothorax oval, scutellum short and pointed posteriorly; metascutum laterally lobate (In.17142).

Forewing: lanceolate, CuP fold prominent extending for 0·6 of wing length, CuA and A close to fold. Sc close to anterior margin, extending approximately to mid-length of wing. R represented by a distal fork. Anal area broad.

Hindwing: linear-lanceolate, with some well-preserved scales (In.25512 + 25252). $Sc + R_1$ well separated from the anterior margin and elongate like CuA; Rs + M apparently with three branches in outer part of wing.

MATERIAL. In.25512 (H) and counterpart In.25252 (H), both Fig. 57; In.17142 (S).

DIMENSIONS. Length of body 1·9 mm, forewing 1·7 mm.

REMARKS. Although rather small, the venation shows some resemblance to the extant lyonetiids *Leucoptera* Hübner and *Bedellia* Stainton; the species probably belongs in the Tineoidea.

Species D

DESCRIPTION. The single specimen consists of the abdomen and incomplete fore- and hindwings. The abdomen tapers to a point posteriorly and the specimen is probably ♀. The forewing is represented by a median fragment and suggests an elongate wing with a discal cell; two oblique branches of R are preserved. A hindwing fragment shows the basal portions of M_3 and of both branches of CuA; M_3 originates very close to CuA_1 and is linked by a short crossvein.

MATERIAL. In.17392 (S).

DIMENSIONS. Length of abdomen 2·7 mm.

REMARKS. The general appearance of this fragmentary fossil is suggestive of the Ditrysia.

Species E

DESCRIPTION. A single dorsal impression of a body and basal half of a forewing. Head rounded anteriorly, thorax typically lepidopterous. Mesoscutellum 0·3 of the length of the mesothorax and rounded posteriorly with traces of the postnotum, suture with mesoscutum gently curved anteriorly; metascutum short with a narrow central portion between the meso- and metascutellum. Abdomen with some traces of segmentation.

Forewing: area between the stem of R and anterior margin moderately wide, Sc well separated from the margin. Base of R_1 closer to R_2 than Sc but well separated from the former. Discal cell moderately narrow. CuA, CuP fold and 1A + 2A close, the last apparently with a basal loop.

MATERIAL. In.25251 (H).

DIMENSIONS. Length of body 3·5 mm, abdomen 2·1 mm.

REMARKS. The affinities of this moth are uncertain but the general appearance suggests that it belongs to one of the 'tineoid' superfamilies.

Species F

DESCRIPTION. A single dorsal impression of the anterior part of the body and the remains of the left wing pair. Head rounded anteriorly. Scutoscutellar suture of mesothorax curved anteriorly, scutellum small and truncate posteriorly. Metathorax elongate with a straight transverse suture with the mesothorax. Abdomen represented by two basal segments.

The wings consist of an incomplete hindwing overlying part of the forewing in which 1A + 2A and the basal loop can be discerned. The venation of the hindwing is more complete and suggests an elongate wing: Sc well separated from the anterior margin, CuA_1 and CuA_2 slightly divergent. M apparently arising on two branches, M_3 equidistant between M_{1+2} and CuA_1. M_{1+2} relatively close to Rs, M_3 continuing into the discal cell. Discocellular crossveins present. Fine transverse lines and some scales are visible on the wing membrane.

MATERIAL. I.9783 (B).

DIMENSIONS. Length of thorax 1·5 mm.

REMARKS. The affinities of this moth are uncertain: the hindwing venation shows some resemblance to *Adela ridingsella* Clemens (Incurvariidae) and *Haplotinea insectella* (Fabricius) (Tineidae).

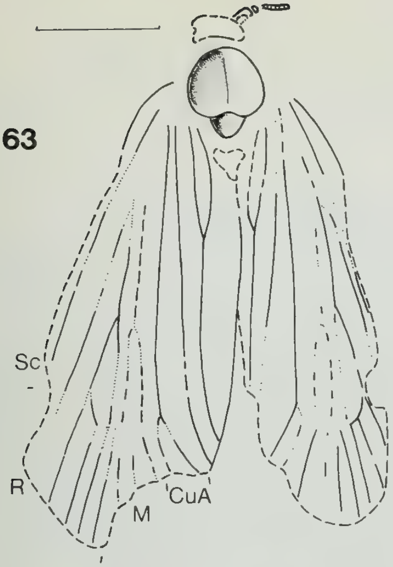
Species G

Fig. 63

DESCRIPTION. A single dorsal mould of the anterior part of the body plus forewings. Antennae typically lepidopterous with pedicel larger than the flagellar segments and an expanded scape. Mesoscutellum pointed posteriorly, and markedly convex (in dorsal view) like the mesoscutum.

Forewings moderately broad and directed posteriorly as in rest position. Estimated original wing length 10·0 mm. Discal cell elongate with traces of M. R_1 originating at 0·35 from the base of the cell, R_2–R_4 from the posterior part of the areole, R_3 closer to R_4. M_1–M_3 and CuA_1–CuA_2

63



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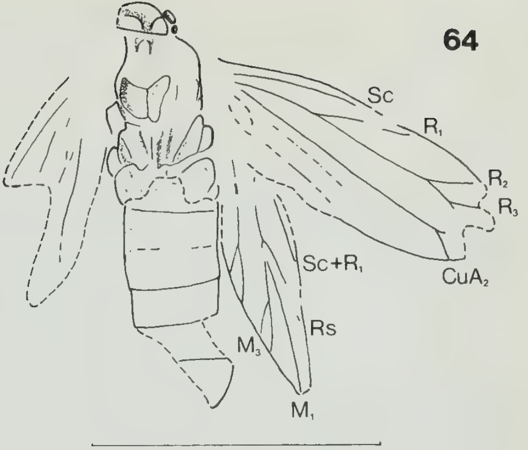
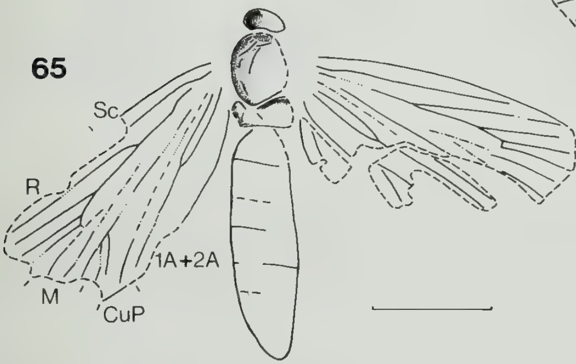
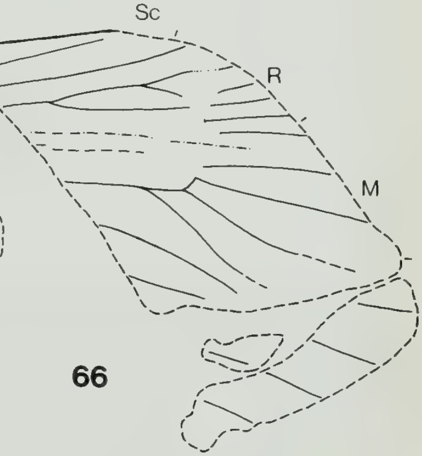

Sc
R_1
R_2
R_3
CuA_2
$Sc+R_1$
Rs
M_3
M_1

65


Sc
R
M
CuP
1A+2A

66



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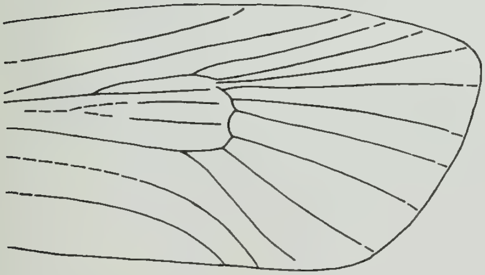

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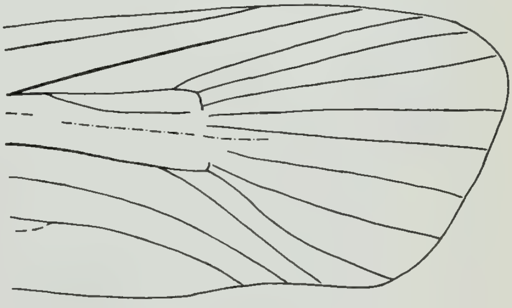

Figs 63–65 Microlepidoptera family uncertain. Fig. 63, species G. I.8917. Fig. 64, species H. I.8809. Fig. 65, species L. In.24506 with details of head and right forewing from counterpart In.64543.
Fig. 66 *Gurnetia durranti* Cockerell, holotype. In.24324. See also Fig. 60.
Fig. 67 *Acrolophus* cf. *cossoides* Felder & Rogenhofer. Recent, Brazil. Outer part of forewing.
Fig. 68 *Culama* sp. Recent, Australia (Meyrick coll. BM(NH) 1938–290). Outer part of forewing.
(Scale line = 2 mm. Figs 66–68 same scale.)

originating close together from the apical end of the discal cell, the origin of CuA_2 less basad than that of R_1. Fine transverse lines present on wing membrane.

MATERIAL. I.8917 (B). Fig. 63.

DIMENSIONS. Length of discal cell in forewing 5·6 mm.

REMARKS. The form of the thorax and primitive venation are very close to that of the tineid genus *Acrolophus* Poëy (cf. Forbes 1923 : fig. 19) but also to the incurvariine *Adela* Latreille (cf. Spuler 1913 : fig. 223).

Species H

Fig. 64

DESCRIPTION. A single ventral impression of the body with wing remains. Head rounded anteriorly. Estimated forewing span 5–6 mm.

Forewing: discal cell elongate and moderately narrow. Sc close to anterior margin and apparently terminating in basal half of wing. R_1 short, originating at 0·3 of the length of the discal cell from base. R_2 and R_3 originating from the apical end of the cell, bases well separated. Only a single branch of CuA is preserved, the base opposite that of R_3. CuP fold slightly closer to CuA than A.

Hindwing: elongate, wing tip attenuate. $Sc+R_1$ close to anterior margin. $Rs+M$ forking near mid-point of wing, M forking a short distance apically; Rs to the outer part of the anterior margin, M_1–M_3 to the outer part of the posterior margin, M_2 and M_3 with common stem. CuA forking opposite $Rs+M$, branches short.

MATERIAL. I.8809 (B). Fig. 64.

DIMENSIONS. Length of discal cell in forewing *c*. 2·0 mm.

REMARKS. The fossil's venation shows some resemblance to that of the gracillariid *Caloptilia alchimiella* (Scopoli) (cf. Meyrick 1928 : figure on p. 788) and some small gelechioids, and it apparently belongs amongst the 'tineoid' superfamilies.

Species I

DESCRIPTION. A single specimen, the body being represented by the abdomen, parts of the thorax and a single leg, all of which are crushed. Estimated forewing span 11–12 mm. Hindwing represented by a median fragment indicating a broad wing, with part of CuA and M_3 preserved. Forewing elongate, over 3·5 times as long as broad, apex unknown. Discal cell relatively narrow, oblique. R_1 originating at 0·45 of the length of the discal cell from base, a short distance basad of the termination of Sc. R_2–R_5, M_1–M_3 and CuA_1–CuA_2 apparently all present and originating from the apical part of the cell, base of R_3 nearly opposite that of CuA_2. $1A+2A$ with basal loop. Forewing covered with numerous well-preserved scales.

MATERIAL. In.64541 (E. A. Jarzembowski & Tertiary Research Group, London). Sticelett Ledge.

DIMENSIONS. Length of discal cell in forewing 3·2 mm, of abdomen 2·8 mm.

REMARKS. The venation resembles extant species of *Gelechia* Hübner, *Plutella* Schrank (cf. Forbes 1923) and *Stegasta* Meyrick; the fossil apparently belongs in one of the 'tineoid' superfamilies.

Species J

DESCRIPTION. A single fragmentary specimen consisting of the thorax and incomplete fore- and hindwings. Forewing elongate, stem of A and CuA close to prominent CuP fold. R with three–four branches preserved in outer half of wing. Sc apparently terminating on anterior margin a little distad of the origin of R_1. Hindwing venation too poorly preserved for comment.

MATERIAL. In.25157 (H).

DIMENSIONS. Length of forewing 3·4 mm.

Species K
Fig. 58

DESCRIPTION. A single ventral impression of the head, thorax and basal part of abdomen with remains of fore- and hindwings. Body elongate, wing membrane with a faint transverse lineation.

Forewing: discal cell elongate with traces of M. Venation complete, R_2–CuA_2 originating from the apical end of the discal cell. Base of R_1 well separated from that of R_2, Sc terminating on anterior margin a short distance beyond the base of R_1.

Hindwing: an incomplete left wing is preserved, anteriorly overlapping the posterior part of the corresponding forewing. $Sc+R_1$ and Rs represented by two short distal fragments. M forking in the discal cell. M_3 linked to CuA_1 by a short crossvein.

MATERIAL. In.25219 (H). Fig. 58.

DIMENSIONS. Length of discal cell in forewing 3·1 mm.

REMARKS. The general habitus is indicative of the 'tineoid' superfamilies and the fossil resembles the extant yponomeutid *Plutella annulatella* (Curtis) (Forbes 1923 : fig. 200), but its exact systematic position is unknown.

Species L
Fig. 65

DESCRIPTION. A single specimen with body, both forewings and fragments of left hindwing. Mesothorax oval with apparent traces of the reduced prothorax anteriorly (In.24506); metascutum short and laterally expanded. Wing membrane with transverse lineation.

Forewing: broad, discal cell elongate with traces of M. R with four branches. R_1 originating at 0·5 of the length of the discal cell from base. R_2 closer to R_3 than to R_1 but well separated from the former. Sc well separated from the anterior margin terminating on the latter just beyond the base of R_2. $R_{4+?5}$, M_{1-3} and CuA_{1-2} originating closely from the apical end of the discal cell, CuA_2 opposite R_3. Fork of $1A+2A$ well separated from posterior margin of wing.

Hindwing: two fragments with vein traces probably of Rs, M, CuA and A.

MATERIAL. In.24506 (H) and counterpart In.64543. Fig. 65.

DIMENSIONS. Length of body 5·8 mm, length of discal cell in forewing 3·2 mm.

REMARKS. The venation resembles that of the extant psychid *Lypusa maurella* (Denis & Schiffermüller) although there is some trace of a chorda in the forewing of the latter (cf. Spuler 1913 : fig. 206). The fossil probably belongs in the Tineoidea.

? Superfamily **COSSOIDEA**
? Family **COSSIDAE**

Genus ***GURNETIA*** Cockerell, 1921

TYPE SPECIES. *Gurnetia durranti* Cockerell 1921, by monotypy.

Gurnetia durranti Cockerell, 1921
Figs. 60, 66

1921*b* *Gurnetia durranti* Cockerell : 473; fig. 38.

HOLOTYPE. In.24324 (H). Figs 60, 66.

DIMENSIONS. Forewing (incomplete) : maximum length 9·4 mm, width 6·5 mm.

REMARKS. The genus and species is known from a single incomplete forewing with associated fragments probably of the hindwing. Estimated original length of forewing 15 mm. The transverse lineation on the membrane (Fig. 60) readily excludes it from the trichopteran family Limnephilidae (cf. Cockerell 1921*b*). Cockerell and Durrant (Cockerell 1921*b*) placed *Gurnetia* in the Cossidae and comparison with Recent material shows that the venation is close to that of the Australian genus *Culama* Walker (Fig. 68). The primitive type of venation shown by *Gurnetia* is also developed in certain microlepidoptera. Cockerell commented on the resemblance to the incurvariine *Nemophora* Hoffmannsegg, but the forewing of this is only about 6–8 mm long. CuA_2 originating close to CuA_1 near the apical end of the discal cell readily excludes the fossil from the Tortricidae. However, the fossil's venation does approach certain genera in the 'tineoid' superfamilies, a possibility not discussed by Cockerell and Durrant (*ibid.*). Thus it resembles the yponomeutid *Orthotaelia sparganella* (Thunberg) which has a maximum forewing length of 13 mm, although the posterior part of the wing is narrower in the latter. It also resembles the extant New World genus *Acrolophus* (Fig. 67), in which wing spans of 30–40 mm are often attained. The placement of *Gurnetia* in the Cossoidea is therefore uncertain although it undoubtedly belongs to the lower Ditrysia.

Superfamily **PYRALOIDEA**
Family **PYRALIDAE**
Subfamily **PYRALINAE**

Genus ***PYRALITES*** Heer, 1856

TYPE SPECIES. *Pyralites obscurus* Heer 1856, by monotypy; Oligocene, Aix-en-Provence.

Pyralites preecei sp. nov.
Fig. 69

DESCRIPTION. Single specimen consisting of decapitated body in dorsal aspect and remains of both fore- and hindwings. Mesothorax oval, scutellum rhomboidal, 0·4 of mesothoracic length. Left tegula distinct. Metascutum typically lepidopterous with two lateral lobes. Abdomen compressed but with some pink calcareous infill showing a number of fine tubular structures. The segmentation of the abdomen is obscure except for the more sclerotized basal segment.

The left wings are partly overlapping, but details of the hindwing venation can be seen beneath the forewing where the posterior part of the latter has flaked away. No trace of colour except some pale brownish pigmentation of the veins; scaly areas may be locally discernible on the membrane.

Forewing: discal cell long and narrow with traces of a median fold. Sc close to anterior margin continuing beyond the end of the discal cell. R producing three branches in outer half of cell, the second branch originating a little nearer the third than R_1. The branches of R and Sc run closely and very obliquely towards the anterior margin but their terminations are not preserved. M_{1-3} curving towards outer margin, M_1 forming an angular fork with the third branch of R, and M_2 originating near to M_3. CuA_1 and CuA_2 diverging from the cell less obliquely than Sc and R branches, CuA_2 separating about midway between R_1 and the second branch of R. The venation suggests a relatively narrow forewing with original length estimated at 15 mm.

Hindwing: anterior margin obscure, discal cell much shorter and broader than in forewing. $Sc+R_1$ prominent, close to Rs for a short distance in distal part of its course. Rs indistinct

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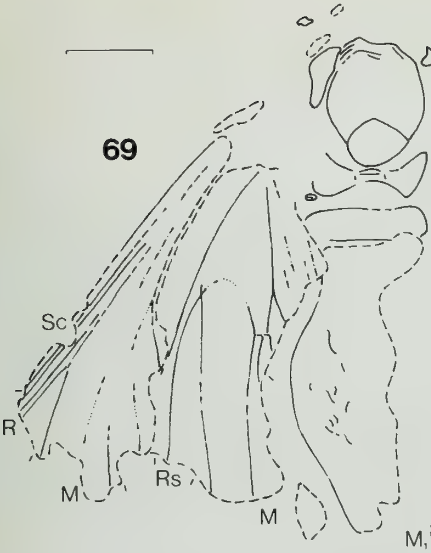
Fig. 69 *Pyralites preecei* sp. nov. **Holotype**, I.8640. Body and left wing pair.
Fig. 70 *Chloroclysta truncata* (Hufnagel). Recent, Britain. Outer part of forewing.
Fig. 71 *Geometridites larentiiformis* sp. nov. **Holotype**, I.8866 and I.8935 (composite drawing).
Fig. 72 *Nymphalites zeuneri* sp. nov. **Holotype**. Fig. 72a, part I.10384; Fig. 72b, counterpart I.10384a. See also Figs 75–76.
Fig. 73 ? Papilionoid, In.64545a.
(Scale line = 2 mm. Figs 69–71 same scale; Figs 72–73 same scale.)



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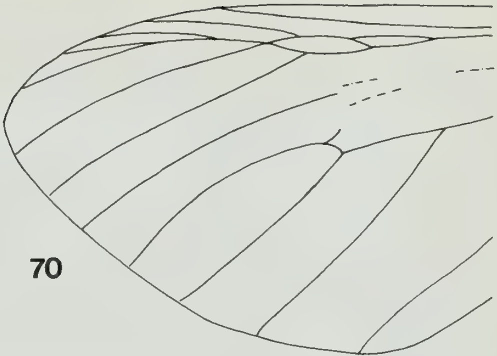

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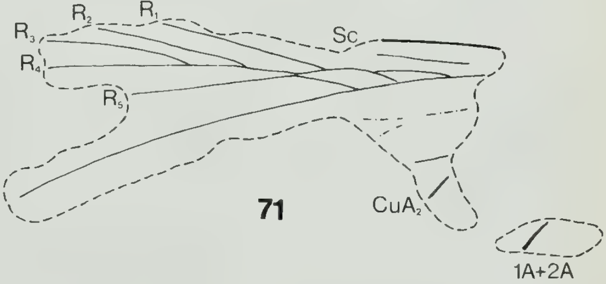
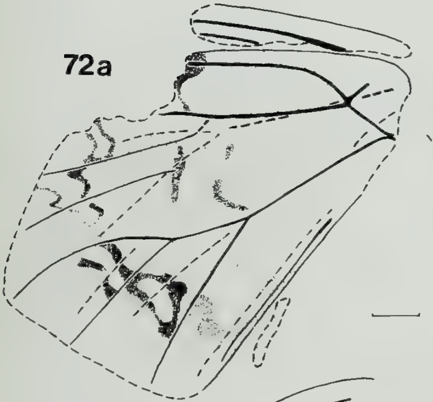
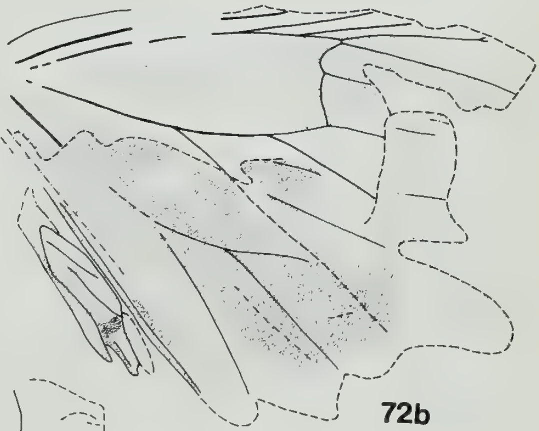


71

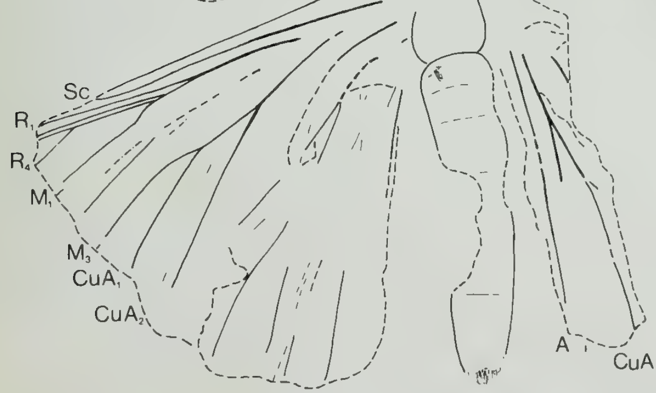
R2
R1
R3
R4
Sc
R5
M1
CuA2
1A+2A



72a



72b



73

Sc
R1
R4
M1
M3
CuA1
CuA2
A
CuA

inwards of the fork with M_1. Bases of M_2, M_3 and CuA_1 closely spaced, apparently linked by crossveins. Only the ends of mdc are preserved, indicating a strong asymmetric basal arch.

The right wings are preserved at an angle of *c.* 15° to the plane of the body, inclined downward and slightly overlapping the abdomen on the same side. They show little useful detail, although a transverse lineation is well preserved.

HOLOTYPE. I.8640 (B). Fig. 69.

DIMENSIONS. Length of mesothorax 3·0 mm, of tegula 1·5 mm.

REMARKS. The general habitus, M absent from the discal cell, M_2 close to M_3 basally in both wings and hindwing with $Sc+R_1$ close to Rs beyond the discal cell are indicative of the Pyraloidea : Pyralidae (Common 1970 : 833, 836). The venation approaches the Recent genera *Paractenia* Ragonot, *Bostra* Walker, *Diloxia* Hampson and *Tyndis* Ragonot (cf. Hampson 1896 : figs 101, 104, 105, 111) in the Pyralinae (and Pyralini of Whalley 1961). The fossil agrees with *Pyralites obscurus* Heer from Aix, southern France (mid-Oligocene, Denizot 1956 : 5) in having a rounded mesothorax, but differs from the latter in the larger size of the mesothorax and in having a distinct mesothoracic scutoscutellar suture (cf. Heer 1856 : 30; pl. 2, fig. 6). However, a re-examination of *P. obscurus* may require a separate genus for *P. preecei* sp. nov.

The adults of Recent pyralids are usually nocturnal insects, pyraline larvae generally feeding on dry or decomposing vegetable material (Bourgogne 1951 : 399–400). The subfamily has a widespread distribution.

Superfamily **GEOMETROIDEA**
Family **GEOMETRIDAE**

Genus ***GEOMETRIDITES*** Clark *et al.*, 1971

TYPE SPECIES. *Geometridites repens* Kernbach 1967, by original designation of Clark *et al.* 1971; Pliocene, Willershausen.

Geometridites larentiiformis sp. nov.
Fig. 71

DIAGNOSIS. A fossil species of Geometridae with the forewing venation resembling that of the extant larentiine *Chloroclysta truncata* (Hufnagel), but differing in that R_{2-5} are not curved apically.

DESCRIPTION. Fragment of a forewing, estimated original length 15 mm. Sc represented by a short median portion. Two elongate areoles present, the inner smaller than the outer; R_{2-5} from apical extremity of latter, the separation of R_1 a little more basad. R_{2-4} with common stem, base of R_2 equidistant between that of R_3 and areole. M_1 gently curved and continuous with stem of R. CuA_2 and $1A+2A$ represented by two short sections, strongly divergent and indicating a broad wing.

HOLOTYPE. I.8866 (B) and counterpart I.8935 (B). Fig. 71.

DIMENSIONS. Length of inner areole 1·5 mm, of outer areole 2·1 mm; fork of R_{3+4} 2·4 mm from latter.

REMARKS. Sc separate from R, two areoles anterior to the apical end of the discal cell, R_5 with areolar origin, and general form of the venation place the wing in the Geometridae in the Sterrhinae or Larentiinae (Common 1970 : 846, 848). The venation is especially close to some Recent Larentiinae (cf. Fig. 70) but the fossil is too incomplete for certain subfamily placing; its clear geometrid affinities render it referable to the broad fossil genus *Geometridites* Clark *et al.*

Both Recent subfamilies have a cosmopolitan distribution, the Larentiinae with a temperate preference (Bourgogne 1951). Geometer larvae are found on foliage, usually pupating in the ground or amongst débris (Common 1970 : 846).

Superfamily **PAPILIONOIDEA**
Family **NYMPHALIDAE**

Genus *NYMPHALITES* Scudder, 1889

TYPE SPECIES. *Nymphalites obscurum* Scudder 1889, by original designation; Oligocene, Florissant.

Nymphalites zeuneri sp. nov.
Figs 72, 75–6

1878 *Lithosia* (sp.); Smith *in* Woodward : 88.
1879 *Lithosia* (sp.); Smith *in* Woodward : 344.
1894*a* Butterfly; Scudder *in* Brodie : 168.
1894*b* Butterfly; Scudder *in* Brodie : 70.
1907 (? *Lithosia*); Handlirsch : 923.
1961 cf. *Euthalia*; Zeuner : 310.

DIAGNOSIS. Medium-sized Palaeogene species of Nymphalidae close to the Recent species *Neurosigma siva* Westwood, *Abrota mirus* Fabricius and *Cymothoe theobene* Doubleday & Hewitson in wing form and venation, but the forewing differs in that M_2 is less close to M_1 basally and the hindwing is differentiated by the short humeral vein towards the humeral angle and relatively narrow anterior area of the wing.

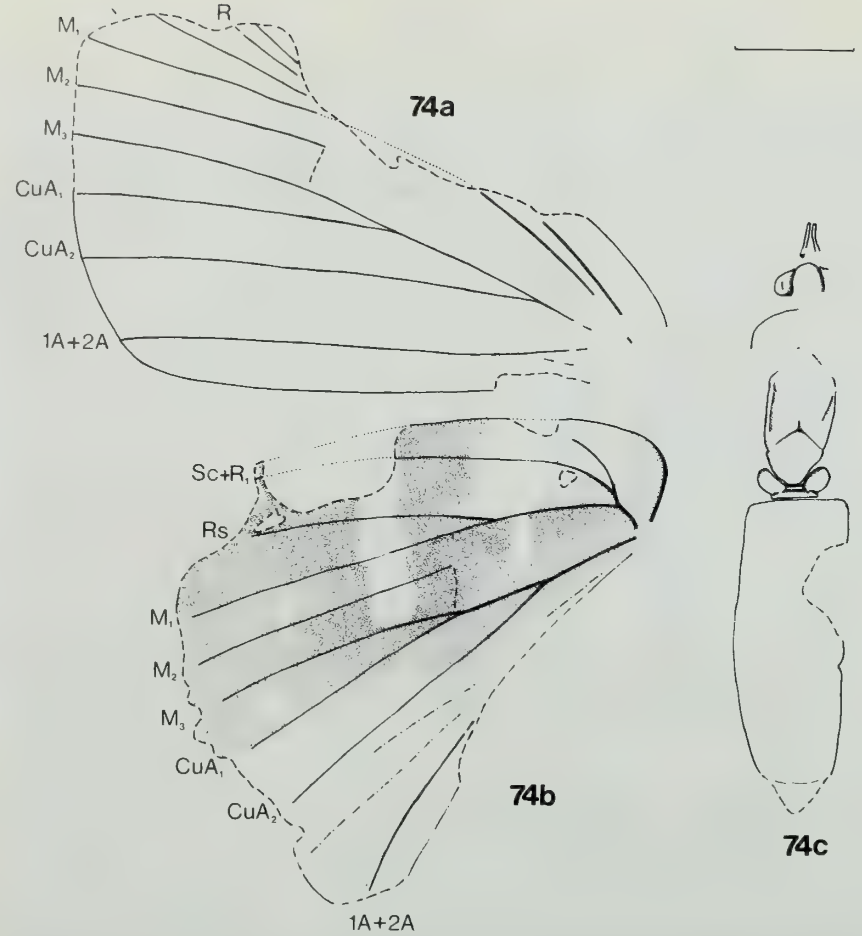
DESCRIPTION. The body is represented by some black chitinous fragments of the thorax near the cleaved edge of the rock, the remainder apparently having broken away during collection.

The remains of both pairs of wings are preserved on the opposite sides of I.10384. The two pairs diverge from the body at an angle of about 15° resembling the upright rest position of the wings in butterflies. However, the hindwings are here overlapped on the outside by the forewings, indicating that they are folded beneath the body as may happen in dead Recent specimens. The two wings on either side are separated from each other at many points by a fine parting of limestone, although this has flaked away in places on I.10384a exposing the forewing. The following account is based on the left pair (Figs 72, 76) as only the bases of the right pair are exposed and these are similar to the left.

Forewing: moderately wide, outer part missing. Discal cell closed, elongate and widest near origin of R_1 with maximum length to width ratio 3·4 : 1. Cells C and Sc moderately narrow. R_1 arising 0·7 of the length of the discal cell from base. R_2 closer to R_{3-5} than R_1 but well separated from the former. R_{3-5} and M_1 arising from the anterior apical angle of the discal cell; stem of R_{3-5} 0·4 of the cell length and only the initial portion of the first fork preserved. Cu trifid, CuA_1 and CuA_2 with relatively divergent courses and separating at 0·8 and 0·5 respectively of the length of the discal cell from base. M_2 closer to M_1 than M_3 at 0·4 of the span between the bases of M_1 and M_3. Branches of M gently curved towards outer margin. Discocellular crossvein fine but clear : udc absent, mdc curved basally and ldc nearly straight. 1A+2A single.

Hindwing: moderately elongate, margins missing except for the basal part of the anterior margin. Discal cell apparently open and broader than in forewing: about 0·66 of the length of the forewing cell. Cell $Sc+R_1$ wide. Humeral area expanded, angular. Humeral vein indicated by a straight groove just over 1 mm long arising from the fork of Sc+R and directed towards the humeral angle. Rs slightly sinuous. M_2 closer to M_1 than M_3. Cu trifid, CuA_1 and CuA_2 divergent arising in the outer half of the discal cell. Inwards of 1A+2A on I.10384a are some traces of wing membrane which apparently include fragments of the anal area, but these are difficult to separate from the right wing pair which is very close at this point. The hindwing shows faint impressed traces of the forewing venation.

Colouration: both wings show a light brown pigmentation which is better preserved in the hindwing. The ventral counterpart of the hindwing shows the underside colour pattern (Fig. 72a). This includes two dark brown lines in the outer part of the discal cell, another traversing cells C and $Sc+R_1$ and an irregular postdiscal band. The last consists of broad crescents with dark


74a
M₁
R
M₂
M₃
CuA₁
CuA₂
1A+2A
74b
Sc+R₁
Rs
M₁
M₂
M₃
CuA₁
CuA₂
1A+2A
74c

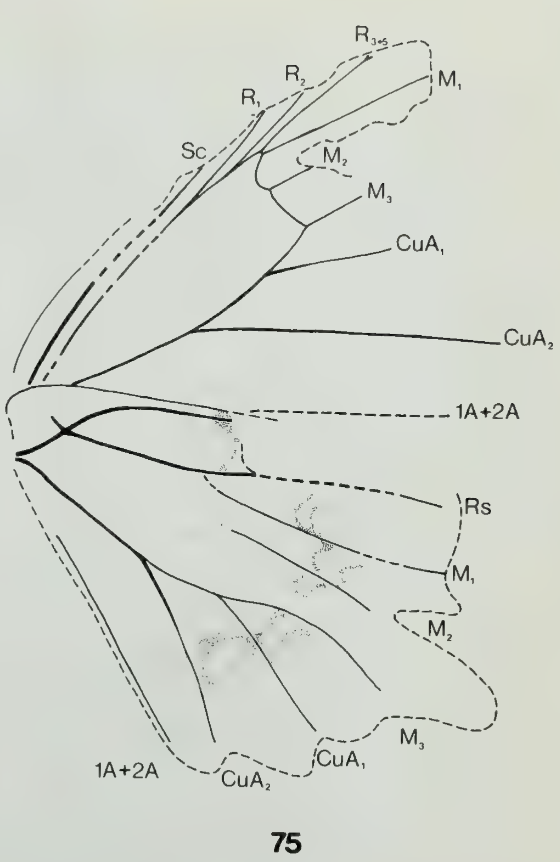

75
R₃₊₅
R₂
R₁
Sc
M₁
M₂
M₃
CuA₁
CuA₂
1A+2A
Rs
M₁
M₂
M₃
CuA₁
CuA₂
1A+2A

Fig. 74 *Lithopsyche antiqua* Butler. Holotype. Fig. 74a, left forewing based on details from part and counterpart. Fig. 74b, left hindwing after removal of forewing on counterpart (I.10369) with some details from part (I.19984). Fig. 74c, body : head and abdomen from counterpart, thorax in dorsal aspect from part. See also Fig. 77.

Fig. 75 Wings of *Nymphalites zeuneri* sp. nov. **Holotype** in ventral aspect, orientation conventional. I.10384. See also Figs. 72a, b, 76.
(Scale line = 5 mm)

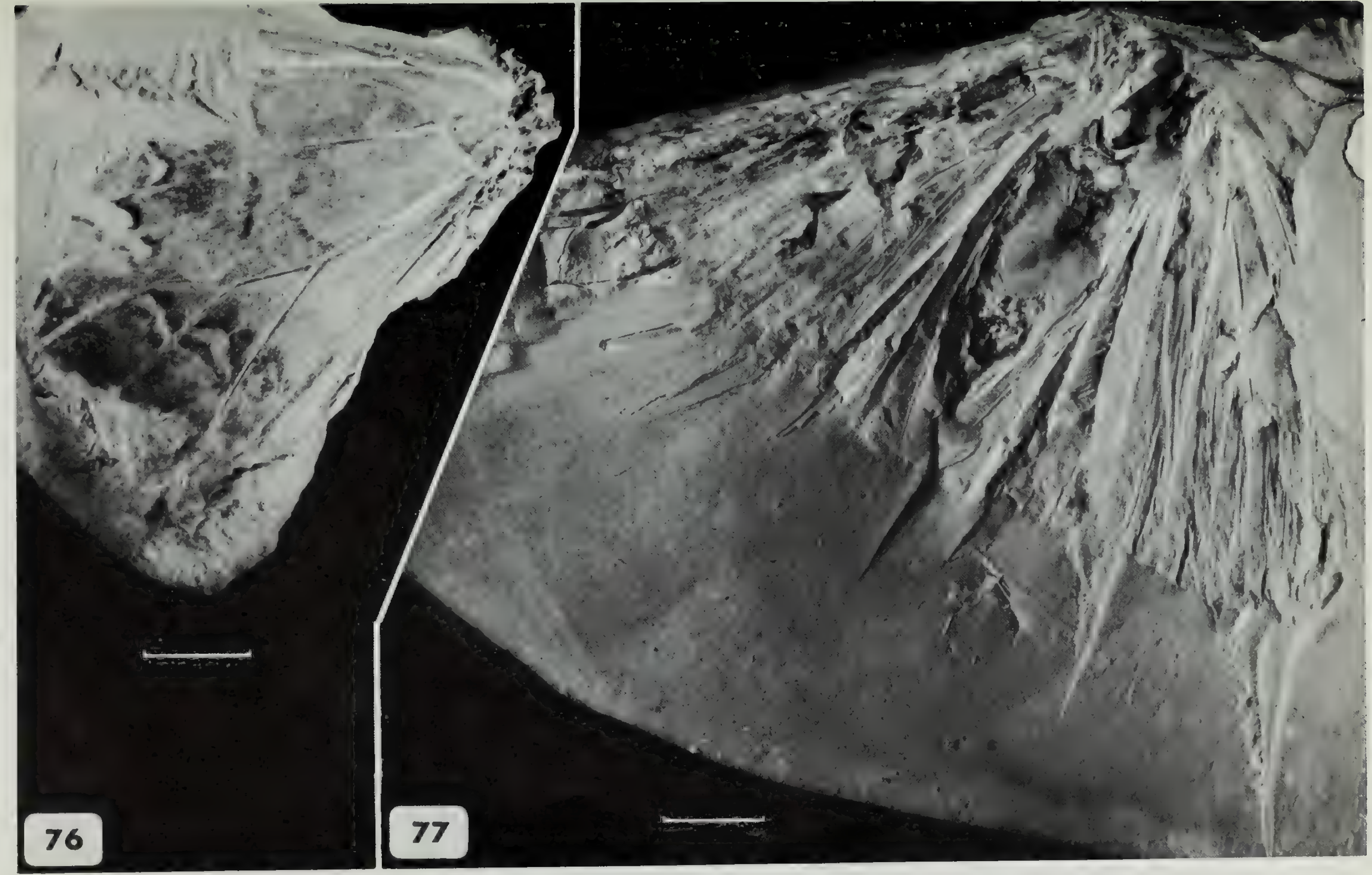


Fig. 76 *Nymphalites zeuneri* sp. nov. **Holotype** (part). I.10384. See also Figs 72a, b, 75.
Fig. 77 *Lithopsyche antiqua* Butler. Holotype (part). I.19984. See also Figs. 74a, b, c.
(Scale line = 5 mm)

brown margins and pale centres; it is interrupted in cell M_2 and offset basally in cell Rs. The discal line in cells C and $Sc+R_1$ shows traces of a pale area near Sc on its outer side.

HOLOTYPE. I.10384 (B) and counterpart I.10384a (B). Figs 72a, b, 75, 76.

DIMENSIONS. *Forewing*: maximum width of discal cell (opposite the base of R_1) 4·0 mm, length 13·5 mm.

Hindwing: base of M_1 to base of CuA_2, 4·4 mm; base of discal cell to base of M_2, 9·2 mm.

REMARKS. The general habitus of the fossil is indicative of the Nymphalidae. Zeuner (1961) regarded it as close to the Recent genus *Euthalia* Hübner, but his proposed description (*ibid.*) was never published. However, a note in the fossil insect collection at the BM(NH) indicates that he regarded it as nearest to the allied *Tanaecia pelea* Fabricius (= *T. pulasara* Moore). This species differs principally from the fossil in that the forewing lacks crossvein ldc and the hindwing has an apically curved humeral vein which originates from $Sc+R_1$ distad of the fork of $Sc+R$ (Schatz & Röber 1885–92 : pl. 26). The absence of ldc in the forewing is also characteristic of *Euthalia* Hübner (Bingham 1905 : 267), the venation of which is very similar to *Tanaecia* Butler (Schatz & Röber 1885–92 : pl. 26). It is possible that Zeuner's comparison with *T. pelea* was based on the large crescentic markings of the postdiscal band in the hindwing of this Malayan species, but the band is more irregular and of a different form in the fossil.

Zeuner (1961 : 310) stated that this is the fossil which Handlirsch recorded as *Lithosia* Fabricius, a living genus of arctiid moth, based on an old label. Handlirsch (1907 : 923), however, queries the identification of *Lithosia* in the Insect Bed and gives Woodward (1879) as the source of the record. Radcliffe-Grote (1901) also doubted the identification. The determinations in Woodward's paper (by F. Smith) were based on material received from A'Court Smith, and although the specimen is from Brodie's collection it is quite likely that it subsequently went to the latter, for Brodie (1878) mentions that he obtained material from A'Court Smith. Specimen I.10384a is actually labelled *Lithosia* in Brodie's hand, but on labels in the same hand accompanying I.10384 the latter is recognized as a butterfly hindwing accompanied by Scudder's name. Brodie (1894*a*, *b*) published the determination made by the latter.

The venation of the fossil does not resemble *Lithosia*, but comes close to that of the living nymphalid species *Neurosigma siva* Westwood, *Abrota mirus* Fabricius and *Cymothoe theobene* Doubleday & Hewitson (Schatz & Röber 1885–92 : pls 24–26). It differs principally in that in these Recent species the forewing appears to have an incipient second anal and M_2 is much closer to M_1 basally; the hindwing has a longer humeral vein which is curved apically and the anterior part of the wing is wider. The venation of the fossil also resembles that of the living *Aeropetes* [= *Meneris*] *tulbaghia* (Linné), but the forewing of the latter differs in that R_2 is closer to R_1, mdc is not curved basally, and in the hindwing the humeral vein has a slight basal curve, M_2 is more central between M_1 and M_3, and ldc is present (Schatz & Röber 1885–92 : pl. 35).

The colour pattern of the fossil does not agree with specimens of the above Recent genera in the collection of the BM(NH) nor with any of the butterflies illustrated in Seitz (1909–39). Of the known Palaeogene genera of Nymphalidae the fossil can only be placed as a separate species in the broadly-based genus *Nymphalites* Scudder.

Personal observations on the decay of the wings of *Inachis io* (Linné) in water indicate that the darker browns remain when the brighter colours have faded. Considering that the wings of other insects in the Insect Bed may preserve a dark brown colouration essentially similar to Recent relatives, e.g. the hemerobiids described herein, it seems likely that the dark brown markings in *Nymphalites zeuneri* are original, with a light centre in the postdiscal band.

Recent Nymphalidae are a large, cosmopolitan family feeding on a variety of angiosperms.

Family **LYCAENIDAE**

Genus ***LITHOPSYCHE*** Butler, 1889

(*non Lithopsyche* Scudder, 1889, = *Lithodryas* Cockerell, 1909)

1889 *Lithopsyche* Butler : 294.

1974 *Calospilites* van Schepdael : 15, 18.

TYPE SPECIES. *Lithopsyche antiqua* Butler 1889 : 294; pl. 21, fig. 3; by monotypy.

Lithopsyche antiqua Butler 1889
Figs 74, 77

DESCRIPTION. *Body*: the head is preserved as a rough cast on the counterpart and shows few details; labial palpi elongate. An external mould of the dorsal surface of the thorax is well preserved in the part; mesothorax elongate, scutoscutellar suture distinct, arcuate; metathorax short, expanded laterally. Abdomen dorsoventrally compressed with scale traces especially at the posterior end.

The following account of the wings is based on the left pair which are well separated from each other by matrix. The right pair are superimposed and their anterior parts are missing; what can be discerned of the venation is similar to the left pair.

Forewing: original span estimated at 60 mm. Costal area moderately wide, Sc represented only by basal portion. Three divergent branches of R are preserved apically. Discal cell elongate, about 0·2 as wide as long. M_{1-3} nearly parallel, with a median M_2 and faint trace of ldc. 1A+2A with traces of a basal fork.

Hindwing: broad, cells C and $Sc+R_1$ expanded. Humeral angle rounded with margin thickened on its inner side. Humeral vein curved apically, originating very close to the separation of $Sc+R_1$. Discal cell short, 0·55 of length of forewing cell. M similar to forewing, CuA_1 separating near the posterior end of ldc. 1A+2A represented by a distal portion and well separated from CuA_2. Anal area largely obscured by the abdomen.

HOLOTYPE. I.19984 (S) and counterpart I.10369 (B). Figs 74a, b, c, 77.

DIMENSIONS. Length of discal cell 15 mm (forewing) and 8·2 mm (hindwing).

REMARKS. Scudder (1883 : 280) used the generic name *Lithopsyche* for a Palaeogene nymphalid from Florissant, but this was a *nomen nudum* and a full description was not published and a type species designated until 1889. In the same year Butler independently described the present genus of geometrid moth from the Insect Bed using the same name, and thus created a homonym. Butler's paper is dated 21st May but was not published until October (Duncan 1937). Scudder's paper has no month of publication although the advertisement with which it is bound is dated 1st October. The original wrapper of the part in which Butler's paper appeared is preserved in the Zoology Library, BM(NH), bound with the journal; the date of issue is given as 1st October. Butler's name therefore would seem to have priority and the replacement name inadvertently offered by van Schepdael to be superfluous and invalid.

Butler saw only the part (I.19984), of which he published a colour lithograph (1889 : pl. 21, fig. 3). Under normal lighting neither half (Fig. 77) shows evidence of the colour banding in Butler's figure, although browns are well preserved in other Insect Bed Insecta. Examination under ultraviolet and infrared lighting only emphasizes some vague traces of pigmentation in the forewing (Fig. 74a). The left hindwing, now exposed on the counterpart, shows some well-preserved brown mottles (Fig. 74b).

Butler compared the fossil with 13 species of extant Geometridae, and specimens of these have been examined. Their only resemblance is that they show much dark pigment in their wing colouration: the venation is quite different. The wing form and venation of *Lithopsyche* Butler is, however, close to that of the extant Riodininae species *Metacharis ptolomaeus* (Fabricius), *Mesene phareus* (Cramer), *Anteros formosus* (Cramer), *Theope publius* Felder, *Uraneis hyalina* (Bates) and *Polystichtis emylius* (Cramer) (Schatz & Röber 1885-92 : pls 43–45; Stichel 1910–11 : pls 8, 13, 15, 22). It differs principally in that there is no evidence of a fork in the outermost branch of R; however, the latter is incomplete in the fossil and a terminal fork may have been developed. The fork is absent in some extant Lycaeninae, e.g. *Neolycaena* de Nicéville.

Recent Lycaenidae are a large, cosmopolitan family feeding on a variety of angiosperms; the larvae are frequently myrmecophilous.

? Superfamily **PAPILIONOIDEA**

Genus **indet.**

Fig. 73

Description. The single specimen consists of a decapitated body with wing remains. The thorax is uncrushed but few details are discernible due to mineralization. Abdomen elongate, flattened dorsoventrally except near base and apex; the lateral interior of the basal segment contains traces of cream-coloured calcified muscle, and the apical segments are covered with a dense coat of piliform scales.

Forewing: (In.64545a, left. Fig. 73). Cells C and Sc moderately narrow. Discal cell elongate, slightly constricted apically and apparently open. Sc terminating on the costal margin a little distad of the end of the discal cell. Branches of M only slightly divergent and gently inclined relative to the long axis of the cell; M_2 nearly equidistant between M_1 and M_3. R_1 originating at 0·7 of the length of the discal cell from base, R_2 and R_{3+4} originating close together where the cell begins to constrict; R_4 parallel to M_1. CuA_1 leaves the cell opposite the base of R_2 and CuA_2 a little basad of base R_1. The posterior part of the forewing is obscured by the corresponding hindwing.

Little further can be said concerning the venation except that the veins immediately to the right of the abdomen (In.64545a) are probably CuA and an anterior anal of the opposite hindwing. There is no indication of colour pattern on the wings although scale traces may be discerned at higher magnification.

Material. In.64545a, b (H). Fig. 73.

Dimensions. Abdomen: length 13 mm. Forewing: estimated original length 20–25 mm; length of R_{3+4} stem, 3·4 mm.

Remarks. The size and venation place the fossil amongst the higher ditrysian macrolepidoptera. The forewing venation bears a general resemblance to some Lycaenidae (cf. Bingham 1907 : figs 72–73), including *Curetis siva* Evans and *Ogyris genoveva* Hewitson, although there are differences in detail. The close proximity of the two outer branches of R resembles certain Nymphalidae, e.g. *Apatura iris* (Linné), although the venation differs in other respects such as in the position of M_2. The fossil probably belongs to the Papilionoidea, though in the absence of further material the placing is uncertain.

The abdominal muscles probably underwent mineral replacement like some seeds from the Insect Bed, where the endospermal cells are replaced by a 'cream-coloured granular substance' (Reid & Chandler 1926 : 7).

Conclusions

During late Eocene and early Oligocene times southern Hampshire and the northern part of the Isle of Wight are considered to have formed part of a wet coastal lowland subject to marine inundation; gradual crustal subsidence resulted in the accumulation of tens of metres of sediment The Bembridge Marls represent one such marine transgression with a much longer regressive period (Daley 1973*a*). Unique conditions near the base of this deposit resulted in the formation of fine-grained limestone in a unit sandwiched between brackish-water clays (*ibid.*), thus preserving the fragile water-logged remains of various small and medium-sized Insecta; the associated biota has already been discussed (p. 239). Insect orders represented are Hymenoptera, Diptera, Coleoptera, Neuroptera, Mecoptera, Lepidoptera, Trichoptera, Hemiptera, Thysanoptera, Psocoptera, Isoptera, Dictyoptera, Orthoptera, Plecoptera, Odonata and possibly Dermaptera. Of these the first three constitute over 70% of the insects in the collections examined, the first two being especially common: more than 120 species of Diptera and Hymenoptera have been described. Although taxonomically diverse, the insects considered in the present paper represent about 1·5% of the total number of insects in the collections examined. The A'Court Smith collection, much of which went to Brodie and to Hooley (p. 239), is biased towards better-preserved material, for Brodie states 'Mr Smith observes that owing to the perverse fracture he has lost a very considerable number of specimens . . .' (Brodie 1878 : 9) The A'Court Smith, Hooley and Brodie collections at the British Museum (Natural History) contain some 9000 insects. A bulk sample collected in 1975 yielded nearly 700 insect remains. Of the orders studied, the numbers of specimens in the main collections compared with the sample (the latter in parenthesis) are: Isoptera 92 (2), Plecoptera 1 (0), Neuroptera 10 (1), Mecoptera 2 (0), Lepidoptera 24 (1). The proportional representation of these orders is therefore broadly similar except in the Isoptera and here the most common species, *Mastotermes anglicus* von Rosen, is a relatively large insect and collector's bias is to be expected.

The Lepidoptera proved the most taxonomically diverse in this study, with 24 species ranging from pollen feeders to non-feeders amongst the adults and both surface feeders and miners amongst the larvae. The Bembridge fauna includes the most primitive Lepidoptera (Micropterigidae) through to the most advanced (butterflies); adult *Micropterix* occurs with its food plants (*Ranunculus*, *Carex*) in the same bed. Of the orders considered here the Lepidoptera are the most diverse in the British and world fauna at the present day with a total of over 165 000 known species. They are usually thought to be very rare as fossils but that is probably partly because the small species are overlooked; however, these specialized terrestrial insects cannot be expected to form a significant part of an aquatic death assemblage. Further work on some of the microlepidoptera from the Insect Bed, such as scanning electron microscope examination for aculae, may help to clarify their affinities. The Neuroptera (Sisyridae excepted) and Mecoptera are represented by families in which both adult and immature stages are terrestrial and, like the Lepidoptera, their infrequency in an aquatic sediment is not surprising. The bionomics of Recent hemerobiids and chrysopids (Neuroptera) are very similar and both are active predators of plant-feeding insects such as aphids and coccids (Balduf 1939 : 250, 292). Aphids are present in the Insect Bed and since the chrysopids and hemerobiids are close to extant forms, it is quite likely that they had a similar ecological role in Bembridge Marls time. The Mecoptera are represented in the Insect Bed only by Bittacidae and there is no evidence of Panorpidae or Boreidae in British Palaeogene strata, the only two families of Mecoptera in Britain at the present day. Carpenter (1954), from a study of Baltic amber, concluded that bittacids were more diverse during the Palaeogene than today, although the virtual absence of resin in the British Tertiaries and its abundance in contemporaneous strata in the Baltic area (Larsson 1978) is somewhat puzzling.

Aquatic insects in the orders studied are represented by the Neuroptera (Sisyridae) and Plecoptera, but these freshwater groups are only known from two incomplete wings of the terrestrial imagines which suggests a limited development of local freshwater habitats; my observations on the Insect Bed Trichoptera tend to support this as the order is relatively rare and taxonomically restricted.

The occurrence of four families of termites indicates a warmer climate than today in the Hampshire Basin during Bembridge Marls time. At the present day their normal poleward limit in the Palaearctic is latitude 45°N (Harris 1970 : 295). Kalotermitids, rhinotermitids and termitids overlap south of about latitude 35 N in the eastern Palaearctic (*ibid.*). In the southern hemisphere the poleward limit of *Mastotermes* is at the Tropic of Capricorn: the northern tropic approximates to the equatorial limit of *Reticulitermes*. The evidence from the termites therefore suggests that, in temperature terms, the palaeoclimate was close to the warm temperate (subtropical)–tropical boundary in the sense of Miller 1961. This is compatible with the evidence from the other groups studied. Daley (1972*b*) has suggested that the Eocene climate of Britain was such as to allow some overlap of modern tropical and temperate biotas and this would facilitate the coexistence of *Reticulitermes* and *Mastotermes*. The Insect Bed Isoptera are represented by alates which only emerge in the open for their ephemeral swarming-flights. The bodies are preserved in many specimens of *M. anglicus*, often with visible appendages, suggesting a fairly local provenance. The occurrence of *Ficus* in the Insect Bed is of ecological interest as this is one of the woody plants which is resistant to attack by extant *Mastotermes*; the occurrence of this termite also suggests that precipitation was less than that of modern rainforest. The Insect Bed termites are represented by wood-feeding forms with one possible exception (p. 253). Modern

Termitidae include many non-lignivorous species and the single detached wing suggests derivation from a more distant habitat, perhaps in more open country.

The British insect fauna in Bembridge Marls time included a number of groups not represented here at the present day. In addition to the Isoptera, other notable absentees include the Bittacidae, Mantispidae and Copromorphidae; the distribution of these and the other taxa is discussed above.

The Insecta are a very diverse group at the present day and were undoubtedly already so in more recent geological times. Many of the characters used by modern entomologists for generic and specific classification are often missing or poorly preserved in fossils. Whilst this does not preclude the possibility of a satisfactory fossil taxonomy, the task of relating Tertiary fossils precisely to their extant relatives is difficult: further collecting and comparative study will probably help to clarify relationships. Meanwhile the fossils provide useful data on Tertiary distribution, ecology and comparative morphology of many modern groups.

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References

Authors of Recent genera and type species are not included.

A'Court Smith, E. J. See Smith.

Balduf, W. V. 1939. *The bionomics of entomophagous insects*, **2**. 384 pp. (1974 reprint) Hampton, Middlesex.

Banks, N. & Snyder, T. E. 1920. A revision of the Nearctic termites with notes on biology and geographic distribution. *Bull. U.S. natn. Mus.*, Washington, **108**. viii + 228 pp., 35 pls.

Bingham, C. T. 1905–07. Butterflies. Pt 1. *Fauna Br. India*, London, (Ent.). xxii + 501 pp., 10 pls. Pt 2. *loc. cit.* viii + 480 pp.

Bosma, A. A. 1974. Rodent biostratigraphy of the Eocene–Oligocene transitional strata of the Isle of Wight. *Utrecht micropaleont. Bull. spec. Publs*, **1** : 1–128, pls 1–7.

—— **& Schmidt-Kittler, N.** 1972. *Ectropomys exiguus* n. gen., n. sp., member of the Otinomyinae n. subfam. (Theridomyidae, Rodentia), from Palaeogene deposits of the Isle of Wight (England) and southern Germany. *Proc. K. ned. Akad. Wet.*, Amsterdam, B **75** : 181–192, pl. 1.

Bourgogne, J. 1951. Ordre des Lépidoptères. *In*: Grassé, P.-P. (ed.), *Traité de Zoologie* **10** (1) : 174–448, pls 1–3. Paris.

Brodie, P. B. 1878. On the discovery of a large and varied series of fossil insects and other associated fossils in the Eocene (Tertiary) strata of the Isle of Wight. *Proc. Warwick. Nat. Archaeol. Fld Club*, Warwick, **1878** : 1–12.

—— 1894*a*. Further remarks on the Tertiary (Eocene) insects from the Isle of Wight and on others from the Lias and Coal Measures. *Geol. Mag.*, London, (2) **1** : 167–169.

—— 1894*b*. Notes on the Eocene Tertiary insects of the Isle of Wight. *Proc. Warwick. Nat. Archaeol. Fld Club*, Warwick, **1894** : 67–70.

Brues, C. T., Melander, A. L. & Carpenter, F. M. 1954. Classification of insects. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **108**. v+917 pp.

Butler, A. G. 1889. Description of a new genus of fossil moths belonging to the geometrid family Euschemidae. *Proc. zool. Soc. Lond.*, **59** : 292–297, pl. 31.

Byers, G. W. 1971. Ecological distribution and structural adaptation in the classification of Mecoptera. *Int. Congr. Ent.*, Moscow (1968), **1** : 486 (only).

Carpenter, F. M. 1931. Revision of the Nearctic Mecoptera. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **72** (6) : 205–277, 8 pls.

—— 1954. The Baltic amber Mecoptera. *Psyche, Camb.*, **61** (1) : 31–40.

Castel, M. 1968. Zones de Charophytes pour l'Oligocène d'Europe occidentale. *C. r. somm. Séanc. Soc. géol. Fr.*, Paris, **4** : 121–123.

Cavelier, C. 1968. L'Éocène supérieur et la base de l'Oligocène en Europe Occidentale. *Mém. Bur. Rech. géol. minièr.*, Paris, **58** : 507–527.

—— **& Pomerol, C.** 1976. Les rapportes entre le Bartonien et le Priabonien. Incidence sur la position de la limite Éocène moyen–Éocène supérieur. *C. r. somm. Séanc. Soc. géol. Fr.*, Paris, **18** : 49–51.

—— —— 1977. Proposition d'une échelle stratigraphique standard pour le Paléogène. *Newsl. Stratigr.*, Leiden, **6** : 56–65.

Chandler, M. E. J. 1964. *The Lower Tertiary floras of southern England.* **IV**. xii+151 pp., 4 pls. London.

Claassen, P. W. 1931. *Plecoptera nymphs of America (North of Mexico).* 199 pp., 36 pls. Springfield, Illinois.

Clark, J., Cole, R., Fawcett, S., Green, M., Howcroft, J., Niedbala, S., Rawlins, K., Theobald, O. & Tobias, M. 1971. Insecta. *Zool. Rec.*, London, **104** (13). xv+704 pp.

Cockerell, T. D. A. 1909. A catalogue of the generic names based on American insects and arachnids from the Tertiary rocks with indications of the type species. *Bull. Am. Mus. nat. Hist.*, New York, **26** : 77–86.

—— 1915. British fossil insects. *Proc. U.S. natn. Mus.*, Washington, **49** : 469–499, pls 60–65.

—— 1917*a*. New Tertiary insects. *Proc. U.S. natn. Mus.*, Washington, **52** : 373–384, pl. 31.

—— 1917*b*. Fossil insects. *Ann. ent. Soc. Am.*, Washington, **10** : 1–22.

—— 1921*a*. Fossil arthropods in the British Museum, V : Oligocene Hymenoptera from the Isle of Wight. *Ann. Mag. nat. Hist.*, London, (9) **7** : 1–25.

—— 1921*b*. Fossil arthropods in the British Museum, VI : Oligocene insects from Gurnet Bay, Isle of Wight. *Ann. Mag. nat. Hist.*, London, (9) **7** : 453–480.

—— 1921*c*. Fossil arthropods in the British Museum, VII. *Ann. Mag. nat. Hist.*, London, (9) **8** : 541–545.

—— 1922. Fossil arthropods in the British Museum, VIII : Homoptera from Gurnet Bay, Isle of Wight. *Ann. Mag. nat. Hist.*, London, (9) **10** : 157–161.

—— **& Andrews, H.** 1916. Dragon-flies from the English Oligocene. *Proc. biol. Soc. Wash.*, **29** : 89–92, pl. 2.

—— **& Haines, F. H.** 1921. Fossil Tipulidae from the Oligocene of the Isle of Wight. *Entomologist*, London, **54** : 81–84, 109–112.

Common, I. F. B. 1970. Lepidoptera. *In*: *The insects of Australia* : 765–866. Melbourne (C.S.I.R.O.).

Crane, M. D. & Getty, T. A. 1975. An historical account of the palaeontological collections formed by R. W. Hooley (1865–1923). *Newsl. geol. Curators Grp*, Keele, **4** : 170–179.

Curry, D. 1958. Palaeogene : England, Wales and Scotland. *Lexique strat. int.*, Paris, **1** (3aXII) : 1–82.

—— 1966. Problems of correlation in the Anglo–Paris–Belgian Basin. *Proc. Geol. Ass.*, London, **77** : 437–467.

——, **Gulinck, M. & Pomerol, C.** 1969. Le Paléocène et l'Éocène dans les Bassins de Paris, de Belgique et d'Angleterre. *Mém. Bur. Rech. géol. minièr.*, Paris, **69** : 361–369.

Daley, B. (1969). *A palaeoenvironmental study of the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire.* Thesis (unpublished), University of Reading.

—— 1971. Diapiric and other deformational structures in an Oligocene argillaceous limestone. *Sedim. Geol.*, Amsterdam, **6** : 29–51.

—— 1972*a*. Slumping and micro-jointing in an Oligocene lagoonal limestone. *Sedim. Geol.*, Amsterdam, **7** : 35–46.

—— 1972*b*. Some problems concerning the early Tertiary climate of southern England. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, Amsterdam, **11** : 177–190.

—— 1973*a*. The palaeoenvironment of the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire. *Proc. Geol. Ass.*, London, **84** : 83–93.

—— 1973*b*. Fluvio-lacustrine cyclothems from the Oligocene of Hampshire. *Geol. Mag.*, London, **110** : 235–242, pls 1–2.

—— **& Edwards, N.** 1971. Palaeogene warping in the Isle of Wight. *Geol. Mag.*, London, **108** : 399–405.

Denizot, G. 1956. Tertiare. *Lexique Strat. Int.*, Paris, **1** (4aVII) : 1–217, 14 maps.

—— 1968. Bartonien, Ludien et Tongrien. *Mém. Bur. Rech. géol. minièr.*, Paris, **58** : 533–552.

Donisthorpe, H. St J. K. 1920. British Oligocene ants. *Ann. Mag. nat. Hist.*, London, (9) **6** : 81–93, pl. 5.

Duncan, F. M. 1937. On the dates of publication of the society's 'Proceedings' 1859–1926. *Proc. zool. Soc. Lond.*, **107** A : 71–84.

Durrant, J. H. See Cockerell, 1921*b*.

Edwards, F. W. 1923. Oligocene mosquitoes in the British Museum, with a summary of our present knowledge concerning fossil Culicidae. *Q. Jl geol. Soc. Lond.*, **79** : 139–155, pl. 7.

Edwards, N. (1966). *A study of the Headon Beds, Osborne Beds and Bembridge Limestone* (*Upper Bartonian and Lattorfian*), *in the Isle of Wight and Hampshire, England.* Thesis (unpublished), University of Reading.

—— 1971. Stratigraphy and correlation of the Headon, Osborne, Bembridge and Hamstead Beds (Palaeogene), Hampshire Basin – a bibliography (1814–1970). *J. Soc. Biblphy nat. Hist.*, London, **6** : 50–60.

Emerson, A. E. 1965. A review of Mastotermitidae (Isoptera), including a new fossil genus from Brazil. *Am. Mus. Novit.*, New York, **2236** : 1–46.

—— 1969. A revision of the Tertiary fossil species of the Kalotermitidae (Isoptera). *Am. Mus. Novit.*, New York, **2359** : 1–57.

Esben-Petersen, P. 1921. Mecoptera. Monographic revision. *Collections Zoologiques de Baron Edm. de Selys Longchamps*, **5** (2). 172 pp., 2 pls. Brussels.

Forbes, E. 1856. On the Tertiary Fluvio-marine Formation of the Isle of Wight. *Mem. geol. Surv. U.K.*, London. xviii + 162 pp., 10 pls.

Forbes, W. T. M. 1923. *The Lepidoptera of New York and neighboring states. Primitive forms – Bombyces.* 729 pp. Ithaca, New York.

Fraser, F. C. 1959. Mecoptera, Megaloptera, Neuroptera. *Handbk Ident. Br. Insects*, London, **1** (12–13). 40 pp.

Fuller, C. 1919. The wing venation and respiratory system of certain South African termites. *Ann. Natal Mus.*, Pietermaritzburg, **4** (1) : 19–102, 9 pls.

Gay, F. J. 1970. Isoptera. *In*: *The insects of Australia* : 275–293. Melbourne (C.S.I.R.O.).

—— **& Calaby, J. H.** 1970. Termites of the Australian Region. *In:* Krishna, K. & Weesner, F. M. (eds), *The Biology of Termites* **2** : 393–448. New York & London.

Grassé, P.-P. 1951. Supre-ordre des Mécoptéroïdes. *In*: Grassé, P.-P. (ed.), *Traité de Zoologie* **10** (1) : 71–124. Paris.

Hampson, G. F. 1896. Moths, 4. *Fauna Br. India*, London, (Ent.). xxvi + 594 pp.

Handlirsch, A. 1906–08. *Die fossilen Insekten und die Phylogenie der rezenten Formen.* 2 vols. ix + 1430 pp., 51 pls. Leipzig.

Handschin, E. 1959. Beiträge zu einer Revision der Mantispiden (Neuroptera). 1. Mantispiden des Musée Royal du Congo Belge, Tervuren. *Revue Zool. Bot. afr.*, Brussels, **59** : 185–227.

Harris, W. V. 1968. Isoptera from Vietnam, Cambodia and Thailand. *Opusc. ent.*, Lund, **33** : 143–154.

—— 1970. Termites of the Palearctic Region. *In*: Krishna, K. & Weesner, F. M. (eds), *The Biology of Termites* **2** : 295–313. New York & London.

Haskins, C. W. 1968. Tertiary Ostracoda from the Isle of Wight and Barton, Hampshire, England. Part II. *Revue Micropaléont.*, Paris, **11** : 3–12, 2 pls.

—— 1971. The stratigraphical distribution and palaeoecological significance of the Ostracoda from the Lower Tertiary Beds of the Hampshire Basin, England. *Bull. Cent. Rech. Pau*, **5** (Supplément) : 545–557.

Heer, O. 1856. Ueber die fossilen Insekten von Aix in der Provence. *Vjschr. naturf. Ges. Zürich*, **1** : 1–40, pls 1–2.

Hill, G. F. 1942. *Termites* (*Isoptera*) *from the Australian Region.* 479 pp., 24 pls. Melbourne.

Hughes, J. C. 1922. *The geological story of the Isle of Wight.* viii + 115 pp., 4 pls, 1 map. London.

Hynes, H. B. N. 1941. The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs. *Trans. R. ent. Soc. Lond.*, **91** (10) : 459–557.

Jackson, J. F. 1933. An outline of the history of geological research in the Isle of Wight. *Proc. Isle Wight nat. Hist. archaeol. Soc.*, Newport, **2** : 211–220.

Jarzembowski, E. A. 1976. Report of Easter field meeting: the Lower Tertiaries of the Isle of Wight. *Tertiary Res.*, London, **1** : 11–16.

Jones, T. R. & Sherborn, C. D. 1889. A supplementary monograph of the Tertiary Entomostraca of England. *Palaeontogr. Soc.* (*Monogr.*), London. 55 pp., 3 pls.

Karsholt, O. & Nielsen, E. S. 1976. *Catalogue of the Lepidoptera of Denmark*. 128 pp. Klampenborg.

Keen, M. C. 1972. The Sannoisian and some other Upper Palaeogene Ostracoda from north-west Europe. *Palaeontology*, London, **15** : 267–325, pls 45–56.

Kellogg, V. L. 1894. The taxonomic value of the scales of Lepidoptera. *Kans. Univ. Q.*, Lawrence, **3** (1) : 45–89, pls 9–10.

Kernbach, K. 1967. Über die bisher im Pliozän von Willershausen gefundenen Schmetterlings- und Raupenreste. *Ber. naturhist. Ges. Hannover*, **3** : 103–108.

Killington, F. J. 1936. *A monograph of the British Neuroptera*, **1**. xix + 269 pp., 15 pls. London.

Kimmins, D. E. 1952. A revision of the genera of the Apochrysinae (family Chrysopidae). *Ann. Mag. nat. Hist.*, London, (12) **5** : 929–944.

Krishna, K. 1961. A generic revision and phylogenetic study of the family Kalotermitidae (Isoptera). *Bull. Am. Mus. nat. Hist.*, New York, **122** : 303–408.

Larsson, S. G. 1978. Baltic amber – a palaeobiological study. *Entomonogr.*, Klampenborg, **1** : 1–192, 12 pls.

McCook, H. C. 1888*a*. A new fossil spider, *Eoatypus woodwardii*. *Proc. Acad. nat. Sci. Philad.*, **1888** : 200–202.

—— 1888*b*. A new fossil spider (*Eoatypus woodwardii*). *Ann. Mag. nat. Hist.*, London, (6) **2** : 366–369.

Machin, J. 1971. Plant microfossils from the Tertiary deposits of the Isle of Wight. *New Phytol.*, London & Cambridge, **70** : 851–872, 2 pls.

McKeown, K. C. & Mincham, V. H. 1948. The biology of an Australian mantispid (*Mantispa vittata* Guérin). *Aust. Zool.*, Sydney, **11** (3) : 207–224, pls 14–15.

MacLeod, E. G. 1970. The Neuroptera of the Baltic amber, 1. Ascalaphidae, Nymphidae, and Psychopsidae. *Psyche, Camb.*, **77** : 147–180.

Martini, E. 1972. Die Gattung *Eosphaeroma* (Isopoda) im europäischen Alttertiär. *Senckenberg. leth.*, Frankfurt a.M., **53** : 65–79, pls 1–2.

Meyrick, E. 1928. *Revised handbook of British Lepidoptera*. vi + 914 pp. Hampton, Middlesex.

Miller, A. A. 1961. *Climatology* (9th ed.). xii + 320 pp. London.

Nakahara, W. 1958. The Neurorthinae, a new subfamily of the Sisyridae (Neuroptera). *Mushi*, Fukuoka, **32** : 19–32, pls 7–9.

—— 1960. Systematic studies on the Hemerobiidae (Neuroptera). *Mushi*, Fukuoka, **34** : 1–69, 16 pls.

Needham, J. G. & Claassen, P. W. 1925. *A monograph of the Plecoptera or stoneflies of America north of Mexico*. 397 pp., 50 pls. La Fayette, Indiana.

Noirot, C. 1970. The nests of termites. *In*: Krishna, K. & Weesner, F. M. (eds), *The Biology of Termites* **2** : 73–125. New York & London.

Pallot, J. See Machin, J.

Pantin, H. M. 1958. Rate of formation of a diagenetic calcareous concretion. *J. sedim. Petrol.*, Menasha, **28** : 366–371.

Parfin, S. I. & Gurney, A. B. 1956. The spongilla-flies, with special reference to those of the western hemisphere (Sisyridae, Neuroptera). *Proc. U.S. natn. Mus.*, Washington, **105** : 421–529, 3 pls.

Piton, L.-E. 1940. *Paléontologie du Gisement Éocène de Menat* (*Puy-de-Dôme*). vii + 306 pp., 26 pls. Paris.

Radcliffe-Grote, A. 1901. Fossile Schmetterlinge und der Schmetterlingsflügel. *Verh. zool.-bot. Ges. Wien*, **51** : 655–661.

Rebel, H. 1935. Bernstein Lepidopteren. *Dt. ent. Z. Iris*, Dresden, **49** : 162–186.

Reid, C. 1889. *In*: Reid, C. & Strahan, A., *Geology of the Isle of Wight*. xiv + 349 pp., 5 pls, 4 appendices. London, *Mem. geol. Surv. U.K.*

Reid, E. M. & Chandler, M. E. J. 1926. *Catalogue of Cainozoic Plants in the Department of Geology. 1 : The Bembridge Flora*. viii + 206 pp., 12 pls. London.

Rey, R. 1967. Essais de corrélations entre bassins Oligocènes de l'Europe occidentale à l'aide des gastéropodes continentaux. *Bull. Soc. géol. miner. Bretagne*, Rennes, **1966** : 1–15.

Riek, E. F. 1970. Plecoptera, Neuroptera, Mecoptera. *In*: *The insects of Australia* : 314–322, 472–494, 636–646. Melbourne (C.S.I.R.O.).

Robinson, G. S. 1977. A taxonomic revision of the genus *Callipielus* Butler (Lepidoptera : Hepialidae). *Bull. Br. Mus. nat. Hist.*, London, (Ent.) **35** : 101–121, 6 pls.

Roonwal, M. L. 1970. Termites of the Oriental Region. *In*: Krishna, K. & Weesner, F. M. (eds), *The Biology of Termites* **2** : 315–391. New York & London.

Rosen, K. von 1913. Die fossilen Termiten : eine kurze Zusammenfassung der bis jetzt bekannten Funde. *Int. Congr. Ent.*, Oxford (1912), **2** : 318–335, pls 26–31.

Schatz, E. & Röber, J. 1885–92. Die Familien und Gattungen der Tagfalter. *In*: Staudinger, O. & Schatz, E., *Exotische Schmetterlinge* **2**. ii + 284 pp., 50 pls. Fürth (Bayern).

Schepdael, J. van 1974. Macrolépidoptères fossiles du domaine paléarctique. *Naturalistes belg.*, Brussels, **55** (1) : 3–37.

Scudder, S. H. 1883. The tertiary lake basin at Florissant, Colo., between South and Hayden Parks. *Rep. U.S. geol. geogr. Surv. Territ.*, Washington, **12** (1) : 271–293, 1 map.

—— 1889. The fossil butterflies of Florissant. *Rep. U.S. geol. Surv.*, Washington, **8** (1) : 433–475, pls 52–53.

—— 1894. See Brodie 1894*a*, *b*.

Seitz, A. 1909–39. *Les Macrolépidoptères du Globe.* (1) **1**, viii + 380 pp., 89 pls (1911); Supplément, vii + 404 pp., 16 pls (1939). (2) **5** (planches), ix pp., 194 pls (1926). (2) **13** (planches), 79 pls (1909). (3) **9** (planches), xii pp., 175 pls (1929). Stuttgart.

Setty, L. R. 1940. Biology and morphology of some North American Bittacidae (Order Mecoptera). *Am. Midl. Nat.*, Notre Dame, Ind., **23** (2) : 257–353.

Smith, E. J. A'Court 1874. Discovery of the remains of plants and insects. *Nature, Lond.*, **11** : 88 (only).

Smith, F. See Woodward, H.

Spuler, A. 1913. *Die sogenannten Kleinschmetterlinge Europas.* cxxvii + 402 pp., 22 pls. Stuttgart.

Stichel, H. 1910–11. Family Riodinidae. *Genera Insect.*, Brussels, **112** : 1–452, pls 1–27.

Stinton, F. C. 1975. Fish otoliths from the English Eocene. Pt 1. *Palaeontogr. Soc.* (*Monogr.*), London. 56 pp., 3 pls.

Tasch, P. 1969. Branchiopoda. *In*: Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **R** : 128–191. Kansas.

Tillyard, R. J. 1931. The wing venation of the order Isoptera, 1. Introduction and the family Mastotermitidae. *Proc. Linn. Soc. N.S.W.*, Sydney, **56** : 371–390, pl. 21.

Tjeder, B. 1959–66. Neuroptera–Planipennia. The Lacewings of southern Africa: 2, Family Berothidae; 4, Family Hemerobiidae; 5, Family Chrysopidae. *S. Afr. anim. Life*, Stockholm, **6** : 256–314, **8** : 296–408, **12** : 228–534.

van Schepdael, J. See Schepdael.

von Rosen, K. See Rosen.

Weesner, F. M. 1970. Termites of the Nearctic Region. *In*: Krishna, K. & Weesner, F. M. (eds), *The Biology of Termites* **2** : 477–525. New York & London.

Whalley, P. E. S. 1961. A change of status and a redefinition of the subfamily Endotrichinae (Lep. Pyralidae) with the description of a new genus. *Ann. Mag. nat. Hist.*, London, (13) **8** : 733–736.

—— 1977. Lower Cretaceous Lepidoptera. *Nature, Lond.*, **266** : 526 (only).

White, H. J. O. 1921. A short account of the geology of the Isle of Wight. *Mem. geol. Surv. U.K.*, London. viii + 201 pp.

Woodward, H. 1878. On the occurrence of *Branchipus* (or *Chirocephalus*) in a fossil state, associated with *Archaeoniscus* and with numerous insect remains in the Eocene freshwater limestone of Gurnet Bay, Isle of Wight. *Geol. Mag.*, London, (2) **5** : 88–89.

—— 1879. On the occurrence of *Branchipus* (or *Chirocephalus*) in a fossil state, associated with *Eosphaeroma* and with numerous insect remains, in the Eocene freshwater (Bembridge) Limestone of Gurnet Bay, Isle of Wight. *Q. Jl geol. Soc. Lond.*, **35** : 342–350, 1 pl.

Zagulyaev, A. K. 1964. Lepidoptera, IV (2). Tineidae, 2 : Nemapogoninae. *Fauna SSSR*, Moscow & Leningrad, (Ent.) **86** : 1–416, pls 1–2. [In Russian; transl. (1968) vii + 436 pp., Jerusalem].

Zeuner, F. E. 1939. *Fossil Orthoptera Ensifera.* xiii + 321 pp., 80 pls. London.

—— 1961. Notes on the evolution of the Rhopalocera (Lep.). *Int. Congr. Ent.*, Vienna (1960), **1** : 310–313.

Zwick, P. 1967. Beschreibung der aquatischen Larve von *Neurorthus fallax* (Rambur) und Errichtung der neuen Planipennierfamilie Neurorthidae fam. nov. *Gewäss. Abwäss*, Dusseldorf, **44–45** : 65–86.

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Synopsis

Recently-collected material of the matoniaceous fern *Phlebopteris braunii* (Goeppert), first described and best known from the Lower Lias of Germany, is described from the Middle Jurassic (Bajocian) of Yorkshire. The Yorkshire leaves are shown to have indusiate sori like the living *Matonia pectinata* R. Br., whereas the Liassic *P. braunii* was firmly believed to have naked sori. Search has however revealed an indusium in Liassic specimens also, and reasons why it had been missed are suggested. *Phlebopteris muensteri* (Schenk 1867) is regarded as a synonym of *P. braunii* and the combined species is renamed *Matonia braunii* (Goeppert) n. comb.

The present status of the Yorkshire Jurassic Matoniaceae is considered. A few specimens of *M. braunii* had been mistakenly identified with other species, blurring their definition. In addition, reasons are given for conserving the specific name *braunii* Goeppert 1841 against names of certain Yorkshire specimens described earlier. The early descriptions of fossil Matoniaceae are also reviewed in general, with notes on the type status of some of the specimens.

Introduction

Fronds agreeing with the well-known Lower Liassic fern *Phlebopteris braunii* (Goeppert) (*P. muensteri* (Schenk)) were collected from the Bajocian of Yorkshire in 1972–73. When suitably prepared the new specimens proved to have indusiate sori like the living *Matonia* whereas *P. braunii* was believed to have naked sori, a position which seemed, at first, confusing. I then realized that certain Yorkshire specimens which I had identified with *Matonidium goeppertii*

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Schenk because they possessed indusia agreed better with the new material. Later still I found that specimens collected from the classic Gristhorpe Bed and described early in the nineteenth century under various names were also similar; see notes on p. 301. Finally I found that *Phlebopteris braunii* itself, from the original localities in the Lias of Bavaria and from East Greenland, also has indusiate sori.

When exposed by splitting the rock, most of the new fronds show their upper surface, and the fertile pinnules only reveal their sori satisfactorily when prepared as transfers. However, a number of Lower Liassic specimens from Bavaria and from Greenland show their lower surface as collected, and since their indusia are in most cases missing the sporangia are seen clearly. There thus seemed no point to early workers, including myself, in preparing transfers of such specimens. Certain Greenland specimens did show sori covered by indusia but when I worked on them 50 years ago I dismissed them as unsatisfactory and kept them merely as duplicates for exchange. Apparently Bavarian collectors did the same. Happily the duplicates were sent to the British Museum (Natural History) and I re-examined them recently, when ready to perceive their nature.

Harris (1931) gave reasons for identifying *Phlebopteris muensteri* (Schenk) with *P. braunii* (Goeppert), a conclusion to which I adhere. The discovery of the indusium, however, distinguishes the combined species from the genus *Phlebopteris*, and it is here placed in *Matonia*, as *Matonia braunii* (Goeppert) n. comb.

Material

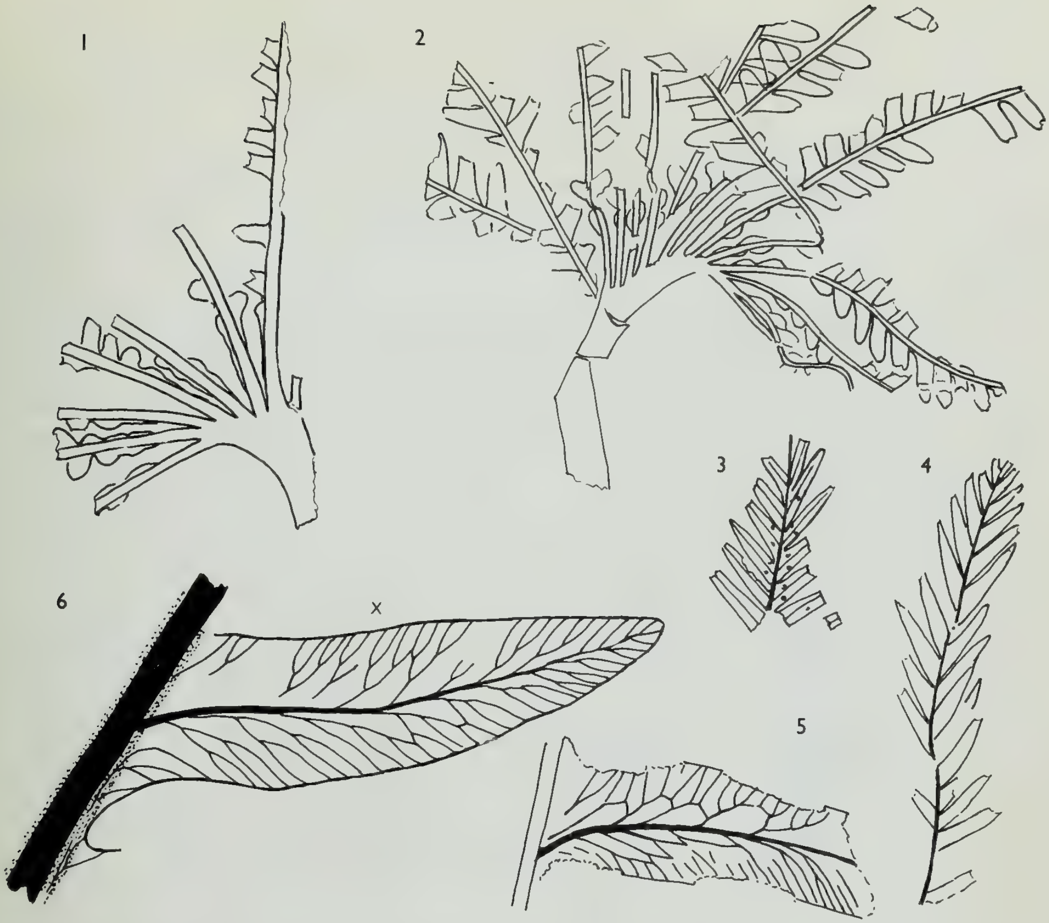
Most of the new specimens were collected from the Hillhouse Nab Plant Bed, Farndale, at about 54°23′3′′N, 0°59′0′′W. This bed was first found in about 1950 and consists of a 2 m thick and rather extensive layer of plant-bearing rocks at the base of the deltaic beds. Like many other Yorkshire plant beds it includes lenticles providing abundant specimens of a particular species and one such lenticle, about 2 m broad and 10 cm thick, gave the specimens described here. This lenticle is the only rich source of *P. braunii* in Yorkshire though material had earlier been collected at Saltwick, also at the base of the deltaics, and from the Gristhorpe Bed at a higher level, but only as occasional specimens.

The Hillhouse Nab matrix is a fragile silty shale and rarely gave blocks more than 20 cm wide. Together with overlap of the crowded fronds this limited the size of the specimens as collected, though some of the fronds may well have been complete when deposited. The matrix is one in which the coaly substance of fern and other leaves with delicate cuticles has become crossed by fine cracks and is apt to crumble away as dust. This is the cause of gaps in drawings of the veins (Figs 5, 6, 15). In most leaves the lamina is opaque but in some layers it had undergone oxidative decay at or following deposition, and the veins show as dark strands on a brown lamina. Otherwise the lateral veins, if seen at all, are marked only by their elongated epidermal cells though the midribs form a small ridge above and a larger ridge below. Most fertile pinnules merely show their sori as obscure bulges on the upper surface and when transferred prove denuded, showing the placenta as a boss. But the best leaves have sori which retain both their sporangia and indusia (though these are apt to be damaged when a transfer is made). Nearly all sporangia were found to be empty when macerated but one was full of ripe spores.

The Gristhorpe and Saltwick specimens are as well preserved as Lower Lias ones and compared with the Hillhouse Nab material the lamina is less completely flattened and the coaly substance more coherent.

Description

Frond form. All the new specimens are somewhat damaged and not one shows a perfect frond centre spread out in a symmetrical fan as in a carefully pressed leaf of *Matonia pectinata*. The specimen in Fig. 1 is the left half of a frond centre, together with a small, probably extraneous axis on the right. The pinna rachises increase in width, left to right, from 1·2 to 1·6 mm and they are borne at the end of a bare 'arm'. Some herbarium specimens of *M. pectinata* in the



Figs 1–6 *Matonia braunii* (Goeppert) comb. nov. Hillhouse Nab, Farndale. Fig. 1. Half of leaf centre, drawn from part and counterpart, V.59743, × 1. The separate axis on right is probably extraneous. Fig. 2. Half of leaf centre, drawn from part and counterpart, V.59744, × 1. Top of rachis twisted and folded. Fig. 3. Apex of fertile pinna, V.59748, × 1. Fig. 4. Apex of sterile pinna, V.59744, × 1. Fig. 5. Venation of small sterile pinnule, shown on imprint of under surface, V.59746, × 6. Vein meshes are numerous in this specimen. Fig. 6. Venation of lowest pinnule from pinna in Fig. 8, p. 298. At × note the branch vein which ends blindly at a point where a placenta might be expected. V.59745, × 5.

BM(NH) show 'arms' bare below and could provide such a fragment. The frond centre in Fig. 2 shows the right half only; the left 'arm' may be folded beneath or missing and the rachis has been folded in compression. Eleven pinnae have rachises about 1·0 mm wide but the two on the right are narrower. None of the specimens contributes to settling the controversial architecture of the frond centre discussed by Hirmer (1927), Hirmer & Hoerhammer (1936), Lundblad (1950) and Appert (1973) as well as others cited by them.

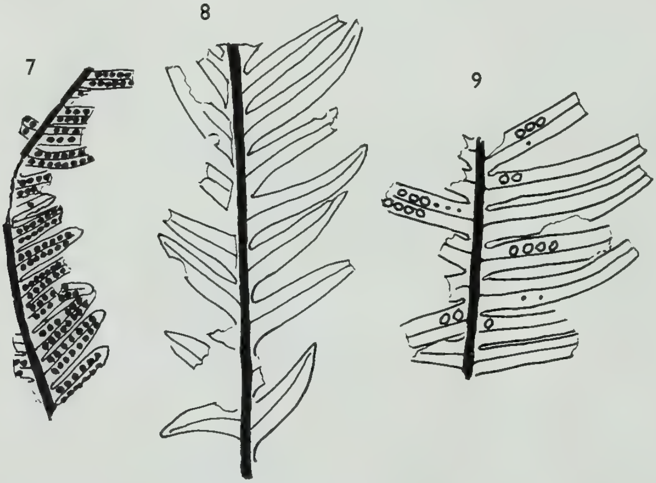
No Hillhouse block gives the full length of a pinna, though from the taper of the rachis I estimate it about 20 cm long. The pinna rachis grades into a wing of lamina, making it hard to measure its width accurately. Over most of a pinna the pinnules remain uniform but at the base they become shorter and broader and finally merge as a continuous wing (Fig. 1). At the apex they become narrower and are borne at a smaller angle, and if fertile they have few sori (Fig. 3). If sterile they look like a *Cladophlebis* with very oblique veins (Fig. 4).

At Hillhouse Nab, where no large leaves are known, the larger pinnae have pinnules 18–25 mm

× 3·5 mm, the smaller pinnae having pinnules 11 × 2·5 mm. In the Gristhorpe Bed pinnules larger than Hillhouse ones occur, along with small ones.

Adjacent pinnules of all specimens are connected by a web of lamina 0·5–1·0 mm wide though this web has often suffered in preservation. The pinnule margins are in contact in some fronds but separated by gaps up to 3 mm wide in others. In fertile fronds and most sterile ones the pinnule margins of the longer pinnules (Figs 7, 9) are parallel to near the apex but in a few sterile fronds the pinnules taper from a broad base (Figs 6, 8); this is the typical '*braunii*' form as distinct from the '*muensteri*' form. Intermediate forms are frequent. The classic Bavarian material named *Laccopteris braunii* (Goeppert 1841) included a remarkable series of small leaves, *L. germinans*, which are generally accepted as belonging to juvenile plants, but the Yorkshire collections include no such specimen.

Sterile Hillhouse pinnules are flat, apart from the raised midrib. In transfers their margins are dark and possibly fibrous. The fertile pinnules are nearly flat but the margins may be slightly depressed. Above each sorus there is a bulge, broad in some pinnae, small in others and never very pronounced. It may be so low that the presence of a sorus is uncertain until a transfer is made. In the Gristhorpe matrix the sterile lamina is slightly convex between midrib and margins and more strongly convex in fertile ones.



Figs 7–9 *Matonia braunii* (Goeppert) comb. nov. Hillhouse Nab, Farndale. All × 1. Fig. 7. Pinna with short, densely fertile pinnules, V.59746. Fig. 8. Sterile pinna with broad-based pinnules, venation shown in Fig. 6, p. 297. Part, V.59745. Fig. 9. Pinna with longer and sparsely fertile pinnules, V.59747.

Venation. In sterile pinnules and in sterile parts of fertile pinnules the veins characteristically fork twice and their branches run obliquely, meeting the margin at 35°. Very occasional veins of large pinnules anastomose, the union being near the midrib or further out and thus irregular (Fig. 5). Many pinnules and all the smaller ones have no anastomosis at all. In the smallest pinnules and in the apical parts of large ones the veins fork only once. In the basal flange along the rachis there is a forward-running branch vein which joins a backward one from the next pinnule, and from the combined vein further branches run to the sinus, though often this part is poorly preserved. All vein branches end in the margin.

In fertile regions of the pinnules each lateral vein has a forward branch ending at the sorus and an outward branch which forks, the branchlet nearest the rachis meeting the margin nearly at a right angle (Fig. 18, p. 302). There are no anastomoses except in the basal web between pinnules.

No vein or rachis shows any hairs or scales, either directly or in transfer.

Sori. Although the upper surface of the lamina is the one exposed in all the Yorkshire specimens, the coaly substance has sometimes crumbled away to reveal sporangia, though I did not recognize

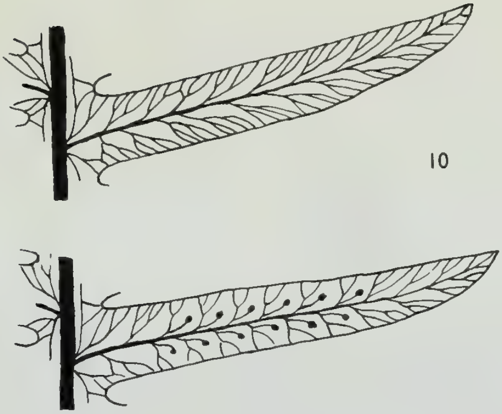


Fig. 10 Diagrams comparing the venation of sterile and partly fertile pinnules of *Matonia braunii*. Note that both are often relatively longer. A higher proportion of sterile veins may anastomose. Fertile pinnules are often more fully fertile, relatively narrower and have narrower webs along the rachis.

the indusium. In transfers of the more perfect fertile specimens the state of the sori varies, even between adjacent sori. In its most perfect state, however, the sorus is entirely covered by the large convex indusium (Fig. 12). Often this is partly broken in preparation and then the outer parts of sporangia are visible; sometimes only the middle of the indusium remains (Fig. 11). More often both indusium and sporangia have been lost, apparently before the preparation was made, and nothing remains but the projecting placenta (Harris 1961: fig. 38D, named *Matonidium*); I consider that this loss occurred before preparation because I believe I can distinguish between the bright surface of coal fractured in preparation and the dull surface of coal preserved in contact with mud. Not one Hillhouse specimen showed a sorus of ripe but undischarged sporangia exposed by the loss of the indusium, though sori in this state have been figured from Bavaria and from Greenland.

Many Hillhouse sporangia were macerated and proved empty but one from an otherwise empty sorus gave a coherent mass of spores (Fig. 14). The maceration failed to separate them but I

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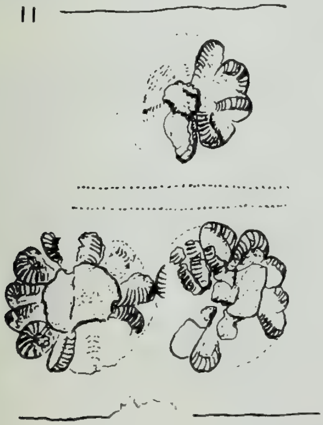

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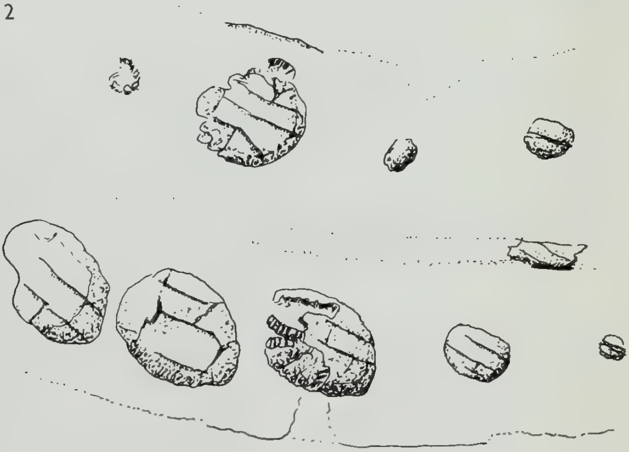
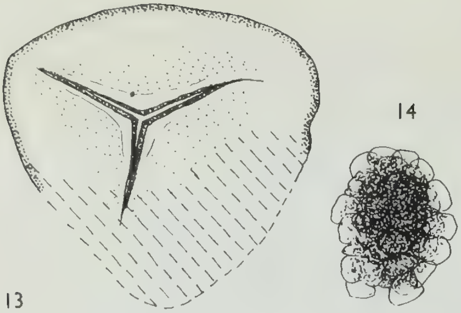


Figs 11–12 *Matonia braunii* (Goeppert) comb. nov. Hillhouse Nab, Farndale. Transfers of fertile pinnules, × 20. Fig. 11. V. 59750. The sori have crumbled in preparation, the upper one having lost its indusium and the lower ones all but some of the middle portion. Fig. 12. V.59751. The indusia are intact apart from cracks caused by shrinking. The small sori to the right are abortive and at the top left there is a denuded placenta.

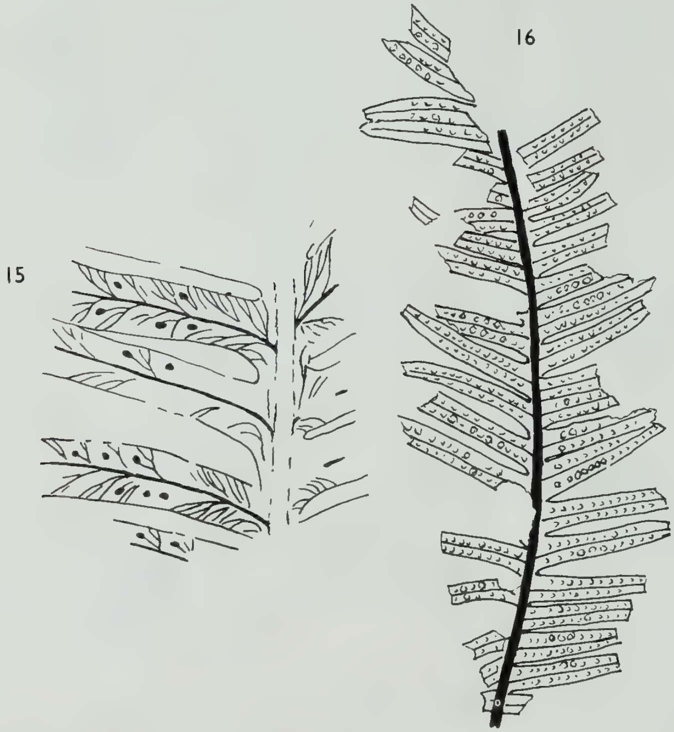


Figs 13–14 *Matonia braunii* (Goeppert) comb. nov. Hillhouse Nab, Farndale. V.59752a. Fig. 13. Spore at the edge of the mass shown in Fig. 14, × 800. The shaded part is obscured by overlapping spores. Fig. 14. Spore mass isolated from a sporangium *in situ*, × 80. Some of the spores are outlined more definitely than is certain.

estimate their number at about 100. The spores have smooth brown walls about 1·5 µm thick and the one most clearly seen (Fig. 13) is figured. They are about 50 µm wide. As the spores are coherent and smooth-walled it is possible that they died before maturing and the fact that this was the only sporangium of the sorus which yielded spores also implies arrested development. Harris (1961) figured a similar spore from a Gristhorpe specimen and a smaller one from a Saltwick specimen, both as *Matonidium*.

Discussion

The indusium. I determined the new specimens in the field as *Phlebopteris braunii* because they agreed in every character visible with a lens. But when I made transfers and found that the sori



Figs 15–16 *Matonia braunii* (Goeppert) comb. nov. Hillhouse Nab, Farndale. Fig. 15. Partly fertile pinna in transfer, V.59749, × 3. The placentae are small and possibly abortive. Fig. 16. Longest available pinna fragment, sori obscure. V.59748, × 1.

had indusia I decided this was impossible. Like others I was convinced that *P. braunii* had naked sori, this being the character that distinguishes *Phlebopteris* from *Matonia*. There seemed a grave practical difficulty. There were two groups of well-preserved specimens, *P. braunii* in the Lower Lias of western Europe and East Greenland in which certain specimens, though a minority, showed naked sori, and the new Yorkshire group in which certain specimens showed indusia when transferred. But most specimens were indistinguishable and this applied also to nearly all those figured previously except the ones showing details of sori. It seemed that the groups were generically distinct but could seldom be distinguished and I tried to escape from the difficulty with elaborate hypotheses.

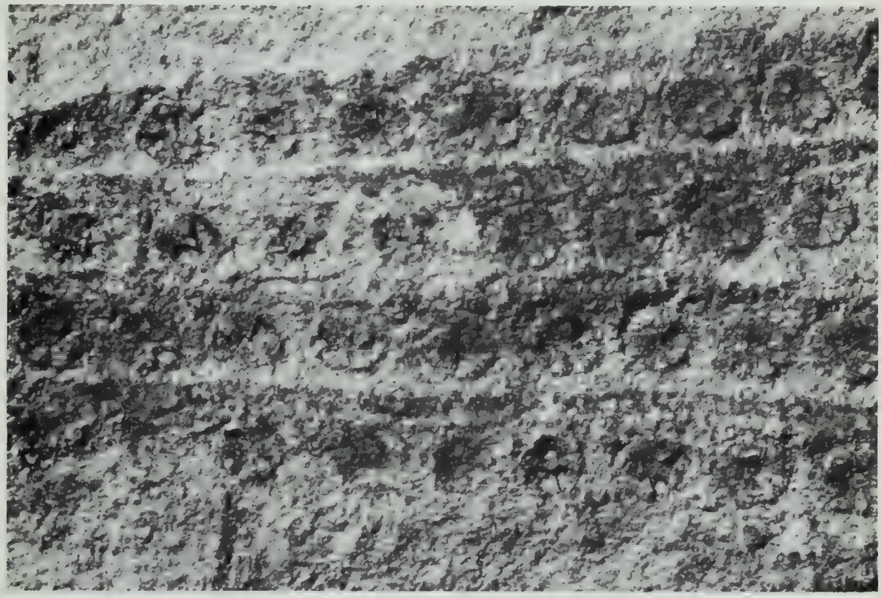


Fig. 17 Two pinnules of *Matonia braunii*, V.21660, Scoresby Sound, East Greenland, × 10. Shrinkage after collection caused cracks to form in the indusium between the sporangia and around the placenta. The sporangia contain ripe spores but their annulus is not visible.

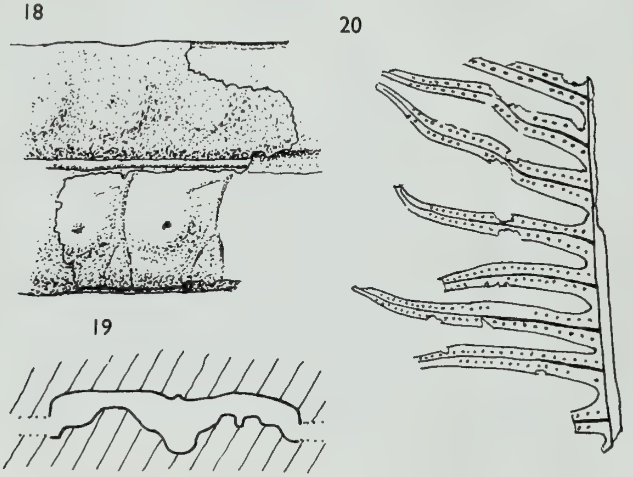
Later, when I saw Liassic specimens of *P. braunii* in the BM(NH) the difficulty vanished. *P. braunii* also has an indusium but is apt to lose it. I suggest that collectors selected against specimens with sori concealed by indusia, as I evidently did in Greenland.

For example, specimen 15043 from Bayreuth, Bavaria, labelled *Laccopteris muensteri*, shows the under-surface of many fertile pinnules, some with intact sori, others denuded. In the intact sori the sporangia form vague bulges but do not show their annulus cells and I conclude that this is because they are covered by an indusium. The evidence is not fully convincing because it is possible that this specimen had been coated with varnish which obliterated them, although I see no sign of any such varnish.

Equally, specimen V.21660, collected by me from the Lower Lias of East Greenland and sent by the Copenhagen Museum in exchange, has sori with an essentially smooth surface though the coaly substance has shrunk since being collected and there is a circular crack around the placenta. There are radial cracks between sporangia but nothing at all of their annulus cells is to be seen (Fig. 17).

There is thus no difference between the indusiate sori of the Yorkshire specimens and the Lower Liassic ones. There is, however, a difference in size between the Yorkshire and the Liassic leaves, recognizable in the pinnules. Those from Hillhouse Nab range from about 12 mm to 25 mm in length and one pinna from the Gristhorpe bed has pinnules 35 mm long. Mature and fertile Liassic leaves also range from about 12 mm upwards, but many specimens are 50 mm or more long; the largest seen (Bavarian) was almost 100 mm × 5 mm. As I can find no other difference I suppose that the Yorkshire environment, particularly at Hillhouse Nab, was unfavourable to the production of very large leaves. The fact that scarcely any unopened sporangia are preserved there suggests that the air may have been dry.

Contour of fertile pinnule. Hirmer & Hoerhammer (1936) illustrated the variation in the surface contour of the fertile pinnule (in specimens named *P. muensteri*), and similar variation has been seen in the Greenland and Yorkshire material. Their pl. 3, figs 3, 3a show a nearly flat upper surface and their pl. 5, fig. 1 a nearly flat lower surface. On the other hand their pl. 3, fig. 6, of the upper surface of another pinnule, shows high mounds above the sori and depressions near the midrib and margins. Their pl. 4, fig. 6 of the under surface is the reverse; the midrib and margins are strongly raised and they are connected by transverse ridges which mark out hollows where the sori were situated. No Yorkshire specimen is as strongly contoured as this, though some approach it.



Figs 18–20 *Matonia braunii* (Goeppert) comb. nov. Gristhorpe Bed, V.31982. Fig. 18. Part of a pinnule of Fig. 20, × 10. The imprint is seen below and to the right, the coaly substance of the lamina above and to the left. Fig. 19. Diagrams representing the contour of the imprints of the pinna of Figs 18 and 20 and an inverted pinna on the same block. Horizontal scale of lower section × 10, of upper × 13, vertical scale increased four times to compensate for matrix compression. Fig. 20. Pinna × 1. The sori are shown as dots representing the placentae, but some in addition show the indusium or the sporangia. A transfer of the counterpart, V.31982a, was figured by Harris (1961: figs 38A-D) as *Matonidium.*

The absolute difference in elevation differs in different matrices; in the Yorkshire specimens it is lower for example in the Hillhouse siltstone than in the Gristhorpe claystone but in each the range is of the same kind. The differences can be explained on Walton's (1936) theory of the changes which occur when a plant organ is compressed in a less compressible matrix, the final form being determined by the surface which originally faced downwards. The original shape of a fertile *M. braunii* pinnule can thus be deduced from the shape of its upper and lower surfaces. Original differences in different pinnules may have occurred also, though it is unnecessary to invoke them to explain what is seen in the fossils.

Specimen V.31982 from Gristhorpe is helpful in working out pinnule contour because it shows three pinnae, two in normal orientation and one inverted, and in all three some of the coal remains but most is missing and the imprint is exposed. By comparison with other blocks I infer that this specimen has the same orientation as when it was part of the Gristhorpe Bed. The imprints and remaining coal are illustrated (Figs 18–20) as seen under very oblique lighting. In describing the imprints I reverse the words 'high' and 'low' as though describing the fossil that made the imprint.

The upper surface (shown by the imprint of the inverted pinnules, Fig. 20 and upper part of 19) has low relief, high regions being at most 100 µm above low ones. The midrib forms a narrow ridge bounded by shallow grooves in the lamina and the margins are depressed. The sori form scarcely perceptible bulges. The lateral veins are sometimes visible as very low ridges. Leaf substance remaining as coal, the original under surface, has just the same relief though the midrib is broader and the placentae and occasionally indusia can be seen (but are nearly flat).

The imprint of the lower surface (shown by the normally orientated pinnules, Fig. 18 and lower part of 19) has relief of up to 200 µm. The broad midrib and the margins are prominent and the sori form conspicuous hollows usually with a central boss, the placenta, sometimes still with the indusium or part of it. One sorus shows the imprint of a full set of sporangia but no indusium. Again the upper surface is mainly just the same but the midrib is narrow and the strong soral bulges often have a dimple above the placenta. The lateral veins may be fairly conspicuous as ridges on the lower surface but the branch to the sorus is usually concealed in the soral pit.

Walton's (1936) theory includes the effects of compression of the matrix. This causes a general and proportionate lowering of relief. Certain pinnules are distorted and tilted, and from their apparent narrowing and the elevation of the raised side I estimate that this sample of the Gristhorpe clay was compressed to about one quarter. I use this figure in reconstructing the original shape of the pinnule (Fig. 19), but unfortunately no laterally compressed pinnule is available to show its original thickness. I have merely made the lamina thick enough to allow for the difference between the deep soral pit below and the low mound above.

The matrix of V.31982 is too coarse to show the imprint of epidermal cells like those illustrated by Appert (1973). He comments (1973: 28) on the difference between his figure of collodion imprints and the figures of Schenk (1867) which apparently represent macerated cuticles. My own efforts to prepare a cuticle from Greenland and from Yorkshire ferns failed. I suggest that Schenk figured a fragment of gymnosperm cuticle which adhered to his specimen.

Identity of *Phlebopteris muensteri* with *P. braunii*. It is convenient to consider this aspect of the taxonomy before identifying the Yorkshire specimens with both. Hirmer (1927) united the two taxa under *Laccopteris elegans* Presl, a species he later placed—with no good reason—in the Marattiales. Hirmer & Hoerhammer (1936), however, separated them and set out the differences in detail. They have been followed in this by most authors, though Kräusel (1958) expressed doubt. On the other hand some have firmly united them under *Phlebopteris muensteri* Schenk, chiefly Harris (1931), Reymanówna (1963), Weber (1968) and Appert (1973). (Goeppert's name *braunii* has priority and possibly these authors mistakenly used *muensteri* because Schenk's fertile specimens were better).

The evidence for identity is simple; the two forms occur together in the field and they intergrade morphologically. Thus they are recorded from the same localities in Bavaria (though I know no details). In Greenland the material was only locally common but was found in five localities and in each the two forms are closely associated (Harris 1931). The two forms also occur together in Yorkshire, particularly at Hillhouse Nab and in the Gristhorpe Bed.

Leaves of the *braunii* form have in fact the appearance of shade leaves. They are always sterile and have a broad, flat lamina showing the veins very clearly. Their pinnules may be triangular and always taper from the base. Leaves of the typical *muensteri* form on the other hand may be sterile or fertile. Their pinnae are long, relatively narrow and parallel-sided to near the apex. The substance of the lamina is thick and the veins are hard to see until a transfer is prepared, when the branching of the lateral veins is seen to be of *braunii* form in sterile pinnules but different in fertile ones. The pinnule margins are often bent downwards in fertile leaves.

Hirmer & Hoerhammer stated additional differences regarded by them as of specific rank but they do not even apply to all the specimens they themselves figured. The most impressive evidence of identity of the two forms is probably from partly fertile specimens, where *braunii* venation is seen in the sterile portions but *muensteri* where there are sori; see for example Harris (1926: text-fig. 6 A, E as '*Laccopteris groenlandica*'; 1961: fig. 37E as *Matonidium goeppertii*) and Fig. 15, p. 300 here.

Identification of Yorkshire specimens. There is no doubt that all the Hillhouse Nab specimens belong to a single species. They are numerous and intergrade, the mean is the most frequent form and the more complete specimens show much of the range of form in the one frond. No similar species is associated with them.

The Gristhorpe Bed specimens are few, though even there a number of fragments may occur on one block. A difficulty is that *Phlebopteris polypodioides* also occurs there and is more frequent, but it is usually easy to distinguish. The specimens accepted as *M. braunii* are like those from Hillhouse Nab but are better preserved and some are larger; one pinna has pinnules 35 mm × 3·5 mm (the largest at Hillhouse Nab was 25 mm × 3·5 mm); if Lindley & Hutton's figure (1831–33: pl. 60) accurately represents *M. braunii* they may be at least 5 mm wide.

At Saltwick a few fragments only were obtained, from a place where it was difficult to collect.

As all of these Yorkshire specimens agree in fine details I identify them with one another confidently.

Reference of *Phlebopteris braunii* to *Matonia*. The genera of Mesozoic Matoniaceae were formerly distinguished on vague and undefined characters, for instance *Matonidium* Schenk on its resemblance in aspect to *Matonia pectinata*. We owe clear distinctions to Hirmer & Hoerhammer (1936). The genera dealt with here differ in a single organ, the indusium. *Phlebopteris* had no indusium at all, *Matonidium* had a placenta which expanded slightly and covered the bases of the sporangia and living *Matonia* has the sorus entirely covered by the indusium. Since *P. braunii* has a large indusium it must be removed from *Phlebopteris* and does not fit *Matonidium*, so the only question is whether it should be placed in the living genus *Matonia*.

Only late in this study did I realize that *Matonia pectinata*, like *P. braunii*, may also show naked sori through loss of the indusium. Seward (1899) figured such a sorus in detail whilst a photograph in Hirmer & Hoerhammer (1936: text-fig. A) shows a herbarium specimen with some sori indusiate and others naked.

I have examined herbarium specimens of *M. pectinata* in the BM (NH) and other herbaria. Fronds with small sori which I presume are immature retain all their indusia but those with full-sized sori nearly all show some sporangia exposed by the loss of the indusium. There is nothing to show whether the indusium dropped off while the frond was alive, as apparently happened in the specimen figured by Seward (1899), or only after it had been dried for the herbarium. But no frond shows all its sori exposed as do certain Lower Liassic ones of *M. braunii*. The excellent Liassic specimens of *M. braunii* showing all their sporangia exposed but still full of ripe spores must be counted as biological failures since they died without releasing their spores, a fate which happens to modern ferns living in continuously damp air. In this respect the Middle Jurassic Hillhouse Nab specimens are more normal since almost every sorus has discharged all its spores.

I can find no account of the behaviour of *Matonia* sori as they ripen. However, I fortunately consulted Mr A. C. Jermy (Department of Botany, BM (NH)) shortly before his recent visit to Sarawak and he gave me the following interesting information about *Matonia* by letter.

> I was able to find it on the mountain ridges of Gunong Mulu. It was growing at about a 5000 ft [1500 m] altitude in those areas which had been bared by land-slips and also partly in glades in the *Lithospermum–Quercus* woodland growing on the crest of the ridges. I looked at many fronds to see if the indusium was falling to expose the sporangium, but in no case did I find this was so. For the most part I should add that the complete sorus was attached, although on many fronds the slightest touch would remove them *in toto*, leaving the characteristic papilla-like receptacle.
>
> I then collected a number of mature fronds and exposed them to the sun. I found that the indusium on these shrivelled or partially folded back thus exposing the very short-stalked sporangia which very soon dehisced.
>
> I also found *Phanerosorus sarmentosus* on this trip. This is a fascinating fern, hanging in festoons against limestone cliffs, with fronds up to 20 ft [6 m] or more. It behaved in the same way as *Matonia* except here there were occasional sori which *had* lost their indusia.

The sori of the leaves described must have been fully ripe, riper than on most of the herbarium fronds I have seen. There is thus a difference of behaviour between our fossil and the living Matoniaceae, but perhaps a slight approach in *Phanerosorus*. Clearly in *M. braunii*, under some conditions in the Liassic at least, the ripe sori may have lost all their indusia before any sporangia dehisced. The fronds were lost from the plant, transported by water and buried with intact sporangia but I cannot tell what interval there may have been between loss of the indusia and of the fronds. I can only imagine that continuous damp weather led to the failure of the sporangia to dehisce, but clearly the difference between *M. pectinata* and *M. braunii* is real. This occurrence of intact sporangia in the fossil Matoniaceae of the Lias is not unique, for in the Yorkshire Oolite many leaves of *Todites williamsonii* and *Klukia exilis* have all their sporangia intact, but containing apparently ripe spores.

M. braunii has much larger pinnules than *M. pectinata* and different venation; in particular its sorus is supplied by a single vein, not several. However, similar differences have been accepted in the fossil genus *Phlebopteris* (the sorus of *P. dunkeri* being supplied just as in *M. pectinata*) and I treat these differences between the living and fossil *Matonia* species as specific rather than generic. It is hard to assess the importance to attach to the different behaviour of the indusia of *M. braunii*, which is partly demonstrable but partly hypothesis, but again I treat it as less than generic. There is a major difference in habitat for it is impossible that fronds should be transported from mountain tops to deltaic pools and buried intact or as large pieces in considerable numbers. Clearly the present observations on the indusium of *M. braunii* call for fresh study of the sori of other fossil Matoniaceae. This study would be best made by transfer preparations of fronds with slightly immature sori facing downwards into the rock. No such study has been made but since in *P. polypodioides* the exposed sorus shows nothing suggesting a central scar, I think there was probably no indusium in this species.

I designate the species as *Matonia braunii* (Goeppert) n. comb. As **lectotype** I designate the specimen named *Laccopteris braunii* by Goeppert (1841: pl. 5, fig. 1), refigured by Schenk (1867: pl. 23, fig. 12) and by Hirmer & Hoerhammer (1936: pl. 2, fig. 1).

Matonia mesozoica Appert 1973, based on abundant, well-preserved material from the Upper Jurassic of Madagascar, is distinguished from *M. braunii* by its short, broad-based and triangular pinnules up to 9 mm × 3 mm. The sterile veins branch twice as in *M. braunii*. Anastomoses, apart from one in the basal web, are rare.

Comparison of *M. braunii* with Yorkshire Matoniaceae. The recognition of *Matonia braunii* called for reassessment of the Yorkshire Matoniaceae in general, and in particular those with indusia, which had been referred to *Matonidium* on this one character. There are changes in three species but these are slight and most of the specimens remain undisturbed: the species are *Matonidium goepperti*, *Phlebopteris woodwardii* and *P. polypodioides*.

The following comparison consists of short statements of the main diagnostic characters of these three species, drawn up as far as possible in the same manner, preceded by a statement of *M. braunii*.

Matonia braunii (Goeppert, 1841), Yorkshire material. Pinnules 12–35 mm × 2·5–3·5 mm, rarely 5 mm, basal connecting web up to 1 mm broad. Substance of lamina dense, sori sunken on lower surface but above forming ill-defined bulges. In basal web a vein anastomosing, other veins in sterile pinnules typically forking twice, branches reaching margin at 40° and at a concentration of 22 per cm, anastomosing only occasionally and then irregularly. In fertile parts of pinnules, lateral vein giving a forward branch to sorus and an outward branch which forks, branchlet nearest rachis almost perpendicular to margin. Indusium present, large but often lost and seldom visible without transfer. Sori at least 1 mm apart.

Matonidium goeppertii (Ettingshausen) Schenk, 1871. Pinnules usually less than 10 mm long and 2 mm wide, web along rachis narrow and with no anastomosing vein. Substance of lamina dense. Upper surface in sterile pinnule slightly convex, in fertile pinnule more convex and sori sometimes forming hemispherical bulges in contact with one another; bulges extending from midrib to margin. Veins once forked in most sterile pinnules, branches reaching margin at about 70° and at up to 50 per cm. In fertile pinnules veins forked, forward branch ending in a sorus, outward branch sometimes forked again near margin and proximal branchlet perpendicular to margin (as in *M. braunii*), but successive sori at less than 1 mm apart.

In Yorkshire *M. goeppertii* is known from the Lower Deltaic only, where it is locally common, but elsewhere it occurs in younger rocks, particularly the Lower Cretaceous. Nearly all the Yorkshire leaves identified as *Matonidium goeppertii* in the BM (NH) agree fully with that species and form a homogeneous group including several excellent specimens. But a few fragments of *M. braunii* were determined as *M. goeppertii* and figured by Harris (1961) because they showed points of interest; they are from the Gristhorpe Bed (Middle Deltaic) and Saltwick (1961: figs 37A–C, E; figs 38A–G). There is now no detailed figure of the sorus of *M. goeppertii* from Yorkshire, nor has its spore been figured from anywhere except at a low magnification. The sori when exposed in transfer look just like the figures of *M. goeppertii* by Hirmer & Hoerhammer (1936), but as happens in *M. braunii* some of them have lost their sporangia and the indusium too, leaving merely a boss representing the placenta.

Phlebopteris polypodioides Brongniart, 1836. Pinnules commonly 40 mm × 5 mm, sometimes larger, basal web often 2 mm broad. Substance of lamina delicate and translucent. Sori not sunken and not projecting above. In basal web an anastomosing vein; veins otherwise essentially similar in sterile and fertile pinnules, laterals at once dividing into forward and backward branches which anastomose to form regular and somewhat rounded broad arches near midrib; sorus situated on primary arch. Branch veins arising from arch and reaching margin at an angle of about 60° and at a concentration of 20 per cm, occasionally branching further and anastomosing. Indusium probably absent.

The specimens now redetermined as *M. braunii* are a few collected from the Gristhorpe Bed in about 1830 and described under various names (see pp. 307–8). They were referred to *Phlebopteris polypodioides* by Seward (1900) and by Harris (1961) but did not fit well.

It should be noted that broad basal arches are not exclusive to *P. polypodioides*, for they occur also in *Piazopteris lorchi* Appert (1973) where the pinnules, though much shorter, have very similar venation.

Phlebopteris woodwardii Leckenby, 1864. (This species is almost always represented by fusainized (charred) pinnule fragments). Pinnules often 5 mm broad, sometimes broader; full length unknown but probably relatively long. Substance of lamina originally dense, preserved as uncompacted charcoal showing individual cells. (Pinna rachis and basal web scarcely known). Veins (not known in basal web) forking and anastomosing to form primary arches which are higher than broad, branch veins arising from arch, forking and sometimes anastomosing, reaching margin at about 80° and a concentration of 50 per cm. Sorus situated in middle of primary vein arch, borne on a forward branch vein. Sorus strongly raised and forming a sharply bounded mound on upper surface, deeply sunken below. (Existence of indusium uncertain and details of sporangia poorly known).

The recognition of *Matonia braunii* in Yorkshire has made it necessary to reconsider the determination of certain unusual fragments determined as *P. woodwardii* which seemed to give additional information about the sorus. These fragments, from Roseberry Topping and from Hawsker, Jack Ass Trod are preserved as coaly compressions and showed *Matonidium*-like sporangia and a small indusium. I still think them rightly determined but the information they gave needs confirmation.

Apart from these compressed fragments, *P. woodwardii* is represented by widespread fusainized pinnule fragments, many of them fertile but all having entirely denuded placentae. They are occasionally abundant, along with fusainized wood. Hirmer & Hoerhammer (1936) removed the species from *Phlebopteris* and placed it in *Nathorstia* of the Marattiaceae, but I do not think that a sorus or synangium of this family would drop off from its placenta, even if scorched by fire. No other Yorkshire leaf is mainly known as fusain.

It is to be noted that this species and *P. dunkeri*, also included by Hirmer & Hoerhammer in *Nathorstia*, are known only as fragments, giving no evidence of the form of the whole leaf.

Distribution of *M. braunii*. Hirmer & Hoerhammer (1936) reduced a huge number of fossil species to six and for two of them, *Phlebopteris braunii* and *P. muensteri*, they gave references to specimens spread over most of the northern hemisphere and ranging in age from the Trias to the Cretaceous. They wrote with such confidence that a reader may think the determination of a matoniaceous fossil from its figure is a clear-cut procedure to well-informed workers, as these two clearly were. But unfortunately it is not. As evidence for this I mention their treatment of the earliest named figure, Phillips' (1829) *Pecopteris caespitosa* (1936: 7). It heads their list for *Phlebopteris braunii* and also their list for *Matonidium goeppertii*, and as redrawn by Seward (1900) it is included in *Phlebopteris polypodioides*. This taxonomic slip arises from real difficulty and had they given *cf.* to each of these taxa, with cross references, I would have thought their treatment perfect.

Their long lists of citations under *P. braunii* and *P. muensteri* are valuable references to specimens of similar aspect. These specimens and later ones can be graded according to the published evidence. The most convincing is an assemblage of specimens showing matoniaceous leaf form with similar venation in sterile and fertile pinnules and no discordant feature. Just three regions produce such material: Bavaria (Franconia) and East Greenland, both in the lowest part of the Lias, and Yorkshire in the Bajocian. If we accept separate pinnae of suitable character we can add Bornholm, Middle or Upper Lias (Möller 1902), and Madagascar, Upper Jurassic (Appert 1973). If we omit the fertile venation (which is often very obscure) there is Poland, ?Upper Lias (Reymanówna 1963), and other localities in the Lower Lias of Bavaria (Kräusel 1958, Weber 1968). These specimens are excellent in other respects. Sikstel' (1960) figures similar pinnae under various names from central Asia (Upper Trias), but details are obscure in the published figures as are those from the Lias of Romania (Semaka 1956). Hirmer & Hoerhammer's citations of unfigured specimens form in my view a category without evidence.

Finally there are some figured specimens cited by Hirmer & Hoerhammer which fail to show the main diagnostic features and in my judgement also show a discrepant character. These include all specimens cited from the Cretaceous and from the Trias older than the Rhaetic, and also those from Asia and Africa.

Field key to the Yorkshire Matoniaceae

This key may fail with exceptional forms though normal forms are likely to occur with them.

1	Specimens (pinnule fragments) preserved as fibrous fusain	*Phlebopteris woodwardii*
–	Specimens preserved as a continuous film of coal	2
2	Pinnules 10 mm × 2 mm or smaller	*Matonidium goeppertii*
–	Pinnules larger than 10 mm × 2 mm	3
3	Pinnules 5 mm or more broad	4
–	Pinnules less than 4 mm broad	5
4	Veins forming broad arches along midrib	*Phlebopteris polypodioides*
–	No arches along midrib, veins forming many small meshes	*Phlebopteris dunkeri*
5	Lamina thick; in sterile pinnule vein branches at a small angle; in fertile pinnule the branches nearly perpendicular	*Matonia braunii*
–	Lamina thin, basal vein arches present	a small form of *Phlebopteris polypodioides*

Notes on fossil matoniaceous leaves described up to 1841

All the specimens cited below are from the Gristhorpe Bed apart from a few whose origin is mentioned.

1828 *'Polypodium'* Murray: 313; pl. 5, fig. 2. Fertile. Specimen not seen but figure looks like *P. polypodioides*.

1829 *Pecopteris caespitosa* Phillips: pl. 8, fig. 10. Specimen in Yorkshire Museum. No description and name therefore not valid. Refigured Phillips 1875: pl. 8, fig. 10 and with descriptive notes on p. 207

together with lign. 20, another specimen (from Haiburn). Original specimen redrawn by Seward (1900: fig. 8) as *Phlebopteris polypodioides*; this determination accepted by Harris (1961). Hirmer & Hoerhammer (1936) determined Phillips' drawing as *Phlebopteris braunii* and also as *Matonidium goeppertii* (1936: 18). Specimen in Phillips 1875: lign. 20 determined by Harris (1961) as *M. goeppertii*. Specimen of Phillips 1875: pl. 8, fig. 10 has its largest pinnules 17 mm × 3 mm, margins slightly depressed, web along pinna rachis narrow, substance of lamina thick and opaque, low bulges at 1 mm intervals perhaps representing denuded sori beneath; venation not observed (fine details damaged by varnish). Certainly not *Matonidium* but agrees well with *Matonia braunii*. I now think it unlikely to be *P. polypodioides* because substance is dense and pinnules are small. A few other Yorkshire Museum specimens determinable with confidence as *P. polypodioides* are labelled *P. caespitosa*.

1829 *Pecopteris crenifolia* Phillips: pl. 8, fig. 11. Drawing shows basal region of specimen in Yorkshire Museum. No description and name therefore not valid. Refigured by Phillips (1875), with description as *Phlebopteris crenifolia* and *P. propinqua* Lindley & Hutton included as a synonym. Specimen well preserved and normal *P. polypodioides*, pinnule margins mostly entire. The broad sori possibly give an illusion of lobing, but scarcely as in the figure. In places there are real bulges in the margin up to 0·5 mm high and these may be opposite sori or between them. At several points, however, the substance at the margins has flaked off or is overlapped by matrix and this gives some appearance of lobing. In the Yorkshire Museum there are also a few other specimens of *P. polypodioides* labelled *crenifolia* Phillips.

1832 or 1833 *Pecopteris polypodioides* Brongniart: pl. 83, fig. 1. Name on plate but description not published until 1836. Sterile pinna showing venation, specimen said to be in Paris.

1833 *Pecopteris polypodioides* Lindley & Hutton: 167; pl. 60 (*nomen nudum* of Brongniart 1828 misapplied). Specimen in Scarborough Museum but not seen by me; venation in figure agreeing with fertile *Matonia braunii*; accuracy of drawing confirmed by Phillips (1875: 202). Figure regarded by Seward (1900) and Harris (1961) as badly drawn *P. polypodioides*. Accepted as *P. braunii* by Hirmer & Hoerhammer (1936). Now accepted by me also as *M. braunii* because I know that leaves with venation as in the figure do occur in the Gristhorpe Bed. This confusing name has never come into use, see below.

1834 *Pecopteris propinqua* Lindley & Hutton: 101; pl. 119. A description and drawing by W. Williamson jr of a specimen collected by W. Williamson sr. Lindley & Hutton never saw the specimen and I have not recognized it in a museum. The figure strongly resembles that of *P. crenifolia* of Phillips, i.e. *P. polypodioides*. Williamson, though, compares it with *P. polypodioides* of Lindley & Hutton, i.e. *Matonia braunii*. The name *propinqua* never came into general use, see p. 309.

1835 *Phlebopteris contigua* Lindley & Hutton: 177; pl. 144. Specimen in good condition in Scarborough Museum. This is the first appearance in print of the genus *Phlebopteris* but it was not defined and therefore not valid. The text shows the authors had seen Brongniart's plate of *P. polypodioides* but supposed that their specimen, in fact typical *P. polypodioides*, was distinct. This name for *Phlebopteris polypodioides* never came into general use and although strictly valid I hope for this reason it will never be revived, see p. 309.

1836 *Phlebopteris* Brongniart: 371. Diagnosis and discussion of genus, first species described as *P. polypodioides*. Species now placed in *Dictyophyllum* were included in the genus.

1836 *Phlebopteris polypodioides* Brongniart: 372 (diagnosis, corresponding to figure, pl. 83, fig. 1, 1a already cited; see 1832 or 1833 above). Generally accepted as the holotype, though description is predated by the scarcely used and less well defined names *P. contigua* and *P. propinqua* of Lindley & Hutton.

1836 *Phlebopteris propinqua* Brongniart: 373; pl. 132, fig. 1; pl. 133, fig. 2. Same figures as *P. crenifolia* Phillips and *P. propinqua* Lindley & Hutton. *P. crenifolia* Phillips cited as synonym.

1836 *Phlebopteris schouwii* Brongniart: 374; pl. 132, figs 4, 4a, 5, 6. Sterile and fertile fragments from Lias of Bornholm. Specimens considered by Möller (1902: pl. 46) as possibly *P. woodwardii* but otherwise indeterminable; accepted by some authors as *P. polypodioides*.

1836 *Polypodites crenifolius* Goeppert: 343, for *Pecopteris crenifolia* Phillips and *Pecopteris propinqua* Lindley & Hutton.

1836 *Polypodites lindleyi* Goeppert: 342; pl. 38, figs 1, 2, for *Pecopteris polypodioides* Lindley & Hutton. Name *lindleyi* applied to a few specimens of *P. polypodioides* in the Yorkshire Museum, but later dropped.

1838 *Laccopteris elegans* Sternberg: 115; pl. 32, figs 1–3, 8a–c. A block showing sterile and fertile pinnule fragments from the Lower Lias of Bavaria. Specimen re-examined by Jung & Knobloch (1972) who remained uncertain about its nature; see p. 309.

1841 *Laccopteris braunii* Goeppert, Lief 1–2 (2): 7; pl. 5, figs 1–7. Lower Lias, Bavaria. The specimen in fig. 1 is considered here to be the Type.

1841 *Laccopteris germinans* Goeppert, Lief 1–2 (2): 9; pl. 6, figs 1–12. Lower Lias, Bavaria. (Widely regarded as leaves of young plants of *L. braunii*).

Summary

This work leaves the validity of three important specific names uncertain.

Is *Laccopteris braunii* Goeppert, 1841 identical with *Laccopteris elegans* Sternberg, 1838? Many have thought so, for example Hirmer (1927), but later he changed his mind and with Hoerhammer (1936) firmly separated *Laccopteris elegans* as a marattiaceous fern with round sori. The matter can only be settled by a fresh study of Bavarian material. If for example specimens matching the original figures were discovered which have unmistakable synangia I would be convinced. At present I am not but leave the name *braunii* standing.

There are still earlier descriptions of *braunii* under other names. Of these, Phillips' (1829) *Pecopteris caespitosa* (see p. 307) is not valid because there is no description. The name *Pecopteris polypodioides* of Lindley & Hutton, 1833, raises a difficult problem. The matter is complicated by the almost simultaneous publication of the relevant works of Brongniart (1828–36) and Lindley & Hutton (1831–37) in numerous parts. Both include descriptions of plants from the Gristhorpe Bed. Another complication is caused by Brongniart's publication of many *nomina nuda* and also of named figures without descriptions, both being completed in later parts. Lindley & Hutton deeply respected Brongniart and co-operated with him and treated his *nomina nuda* as valid names, even when unsure how they applied.

The first matoniaceous fern of Brongniart, 1828, is his *nomen nudum Pecopteris polypodioides*. The first description in valid form is of a fertile pinna showing the specific character of *braunii* by Lindley & Hutton (1833: pl. 60). The description is good but unfortunately they misapplied Brongniart's *nomen nudum* to their specimen. The words '*Pecopteris polypodioides*' head their text but just beneath in the synonymy they give '?*P. polypodioides* Brongniart p. 57'. In the text they say: 'It is evident that our fossil is referable to Adolphe Brongniart's genus Pecopteris; but as the figures illustrative of that genus are not yet published, we have no means of knowing to what species; we conjecture only that it must be his *P. polypodioides*, from the aptness of the name, and from its having been procured by him from the Lower Oolite'. Soon after they wrote this, Brongniart's (1832 or 1833) named figure of *P. polypodioides* was published and their error was plain. They had a new species. Can we accept Lindley & Hutton's expressed doubt as making the application of the name *polypodioides* to their specimen infirm and therefore not valid in nomenclature? It would be greatly in the interests of palaeobotany to do so and this is the view I take. So *polypodioides* L. & H. is not after all the first valid name of *braunii*. But some may disagree.

I turn to *P. polypodioides* of Brongniart. Its earliest named figure, *Pecopteris crenulata* Phillips, 1829, has no description. After Lindley & Hutton had seen Brongniart's (1832 or 1833) figure they received Williamson's drawing which they published (1834: pl. 119) under the name *Pecopteris propinqua*. They recognized that the veins were as in *P. polypodioides* of Brongniart, but considered that the lobed margins of the pinnules distinguished it. I suppose that the specimen is like Phillips' drawing of *P. crenulata*, a fertile pinna where the figure gives an exaggerated impression of lobes and that it is merely a somewhat inaccurate drawing of *polypodioides* Brongniart, but as I have not seen the specimen I cannot be as sure as I am about Phillips' very similar figure. The next validly published name is *Pecopteris contigua* Lindley & Hutton, 1835: pl. 144. The figure and the specimen itself show the venation of a typical specimen of *P. polypodioides* but Lindley & Hutton thought that its crowded pinnules distinguished it. All later authors have considered it well within the form range of *P. polypodioides* and have dropped the name *contigua*, though I can see no way in which this can be done in accordance with the Code.

Thus as I see it, the name *braunii* (or *elegans*) is saved, though by a narrow margin, from becoming '*polypodioides* L. & H.'. But the valid name for Brongniart's species is either *propinqua* L. & H. or *contigua* L. & H.

I have never flouted the Botanical Code but may have breached it inadvertently. But now I continue to use the name *polypodioides*. To change it wastes time and causes frustration. Palaeobotanists will be aware that there is nothing basic in taxonomy that makes this change of name necessary. There are only the provisions of the Code and rulings of Botanical Congresses against the conservation of any specific name, though they did agree to conserve generic names. Had these fossils been animals there would have been little difficulty. The zoologists (including palaeontologists) can and do conserve old specific names. They could have surmounted the trouble caused by *polypodioides* L. & H. in that way, but I suppose they could, as an alternative, have deemed that Brongniart's drawing was published slightly earlier (as it may have been) and accepted it as a valid characterization of the species, cutting out the Lindley & Hutton figure and name and making *propinqua* and *contigua* synonyms.

I state the facts as I see them and leave the name *Phlebopteris polypodioides* standing and merely express the hope that before anyone changes it, the Botanical Code will be altered in a way which will make this name regular.

These nomenclatorial difficulties began through ordinary taxonomic errors. I think they were at first perpetuated through the early palaeobotanists having in their minds principles other than that of priority of publication, or at least they did not give that overwhelming weight. To some, admiration for Brongniart's masterly work was a reason for preferring his names to ones published a year or two earlier. Much later, Seward in his revisions of Mesozoic floras was unwilling to put nomenclatorial priority over the advantages of letting a well-understood name continue to stand; that is on his own judgement he conserved specific names. These names still stand.

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References

Appert, O. 1973. Die Pteridophyten aus dem Oberen Jura des Manamana in Südwest-Madagaskar. *Schweiz. paläont. Abh.*, Basel, **94** : 1–62, 90 pls.

Brongniart, A. 1828. *Prodrôme d'une Histoire des Végétaux fossiles.* viii + 223 pp. Paris.

—— 1828–38. *Histoire des végétaux fossiles, ou recherches botaniques et géologiques sur les végétaux renfermés dans les divers couches du globe.* **1.** xii + 488 pp, 171 pls. Paris. Parts cited (dates taken from Zeiller 1903: 306) Liv. 7: 265–288, pls 83–97, 1832 or 1833; Liv. 11: 369–416, pls 135–146, 1836.

Goeppert, H. R. 1836. Die fossilen Farrnkräute (Systema filicum fossilium). *Nova Acta physico-med.*, Halle a.S., **17** (Suppl.). xxxiii + 488 pp., 44 pls.

—— 1841–46. *Die Gattungen der fossilen Pflanzen vergleichen mit denen der Jetzwelt und durch Abbildungen erlautert.* 151 pp., 51 pls. Bonn.

Harris, T. M. 1926. The Rhaetic Flora of Scoresby Sound, East Greenland. *Meddr Grønland*, Copenhagen, **68** : 45–148, pls 1–13.

—— 1931. The Fossil Flora of Scoresby Sound, East Greenland. 1. Cryptogams (exclusive of Lycopodiales). *Meddr Grønland*, Copenhagen, **85** (11) : 1–102, pls 1–18.

—— 1961. *The Yorkshire Jurassic Flora*, **1.** *Thallophyta–Pteridophyta.* ix + 212 pp. London, Brit. Mus. (Nat. Hist.).

Hirmer, M. 1927. *Handbuch der Paläobotanik.* xvi + 708 pp., 817 figs. Munich & Berlin.

—— **& Hoerhammer, L.** 1936. Morphologie, Systematik und geographische Verbreitungen der fossilen und rezenten Matoniaceen. *Palaeontographica*, Stuttgart, B **81** : 1–70, pls 1–10.

Jung, W. & Knobloch, E. 1972. Die 'STERNBERG-Originale' der Bayerischen Staatssammlung für Paläontologie und historische Geologie zu München. *Mitt. bayer. St. Paläont. Hist. Geol.*, Munich, **12** : 105–111.

Kräusel, R. 1958. Die Juraflora von Sassendorf bei Bamberg. *Senckenberg. leth.*, Frankfurt a.M., **39**, 1–2: 67–102, pls 3–8.

Leckenby, J. 1864. On the sandstones and shales of the Oolites of Scarborough, with descriptions of some new species of fossil plants. *Q. Jl geol. Soc. Lond.* **20** : 74–82, pls 8–11.

Lindley, J. & Hutton, W. 1831–37. *The fossil flora of Great Britain; or, figures and descriptions of the vegetable remains found in a fossil state in this country.* **1** (1831–33), li + 223 pp., pls 1–79. **2** (1833–35), xxvii + 208 pp., pls 80–156. **3** (1835–37), 208 pp., pls 157–230. London.

Lundblad, A. B. 1950. Studies in the Rhaeto-Liassic floras of Sweden. 1. Pteridophyta, Pteridospermae and Cycadophyta from the mining district of N.W. Scania. *K. svenska VetenskAkad. Handl.*, Stockholm, (4) **8** : 1–82, pls 1–13.

Möller, H. 1902. Bidrag till Bornholms fossila flora. Pteridofyter. *Acta Univ. lund.* **38** 2 (5) : 1–63, pls 1–6.

Murray, P. 1828. Account of a Deposite of Fossil Plants, discovered in the Coal Formation of the Third Secondary Limestone, near Scarborough. *Edinb. new phil. J.* **5** : 311–317, pl. 5.

Phillips, J. 1829. *Illustrations of the Geology of Yorkshire, or a description of the strata and organic remains of the Yorkshire coast* (i.e. Part 1, 1st edn). xvi + 192 pp., 9 + 14 pls. York.

—— 1875. *Illustrations of the Geology of Yorkshire; or, a description of the strata and organic remains. Part I, The Yorkshire Coast.* (3rd edn, ed. Etheridge, R.) xii + 354 pp., 28 pls, map. London.

Reymanówna, M. 1963. 1. Review of investigations on Polish Jurassic floras. 2. The Jurassic flora from Grojec near Cracow in Poland, Part I. *Acta palaeobot. Cracov.* **4** (2) : 1–48, pls 1–9.

Schenk, A. 1865–67. *Die fossile Flora der Grenzschichten des Keupers und Lias Frankens.* xxiv + 232 pp., Atlas 45 pls. Wiesbaden.

—— 1871. Beiträge zur Flora der Vorwelt, IV. Die Flora der nordwestdeutschen Wealdenformation. *Palaeontographica*, Stuttgart, **19** : 203–262, pls 22–43.

Semaka, A. 1956. Contribuţii la Flora Liasică de la Vulcan-Codlea. Nota II. *Buletin sti. Acad. Republ. pop. Rom.* (ser. Geol. Geogr.), Bucharest, **1** (1–2) : 107–121, figs 1–30.

Seward, A. C. 1899. On the structure and affinities of *Matonia pectinata* R. Br. with notes on the geological history of the Matonineae. *Phil. Trans. R. Soc.*, London, B **191** : 171–209, pls 17–20.

—— 1900. The Jurassic Flora. I, The Yorkshire Coast. *Catalogue of the Mesozoic Plants in the Department of Geology, British Museum (Natural History).* **3**, xii + 341 pp., 21 pls. London.

Sikstel', T. A. 1960. [Stratigraphy of the continental deposits of the upper Permian and Triassic of Central Asia.] *Trudȳ tashkent. gosud. Univ.* (n.s.) **176** : 1–147, pls 1–19 (numbered as pages). [In Russian].

Sternberg, C. von 1820–38. *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt.* 200 pp., 70 pls col. Leipzig & Prague.

Walton, J. 1936. On the factors which influence the external form of fossil plants; with descriptions of the foliage of some species of the Palaeozoic Equisetalean genus *Annularia* Sternberg. *Phil. Trans. R. Soc.*, London, B **226** : 219–237, pls 31, 32.

Weber, R. 1968. Die fossile Flora der Rhät-Lias-Übergangsschichten von Bayreuth (Oberfranken) unter besonderer Berücksichtigung der Coenologie. *Erlanger geol. Abh.* **72** : 1–73, pls 1–17.

Zeiller, R. 1903. Flore fossile des Gîtes de Charbon du Tonkin. viii + 328 pp., 56 pls. *Étud. Gîtes minér. Fr.*, Paris.

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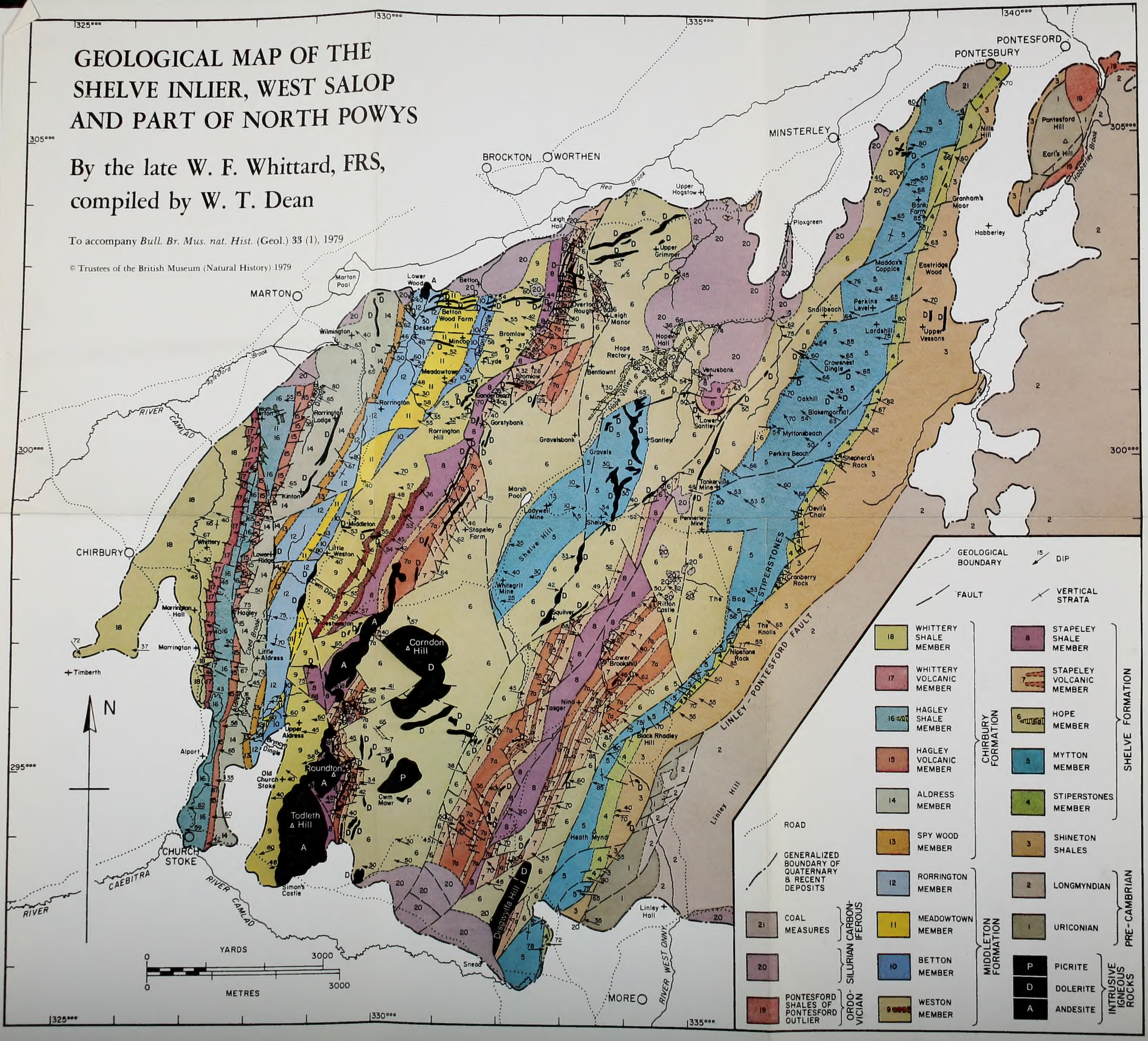
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